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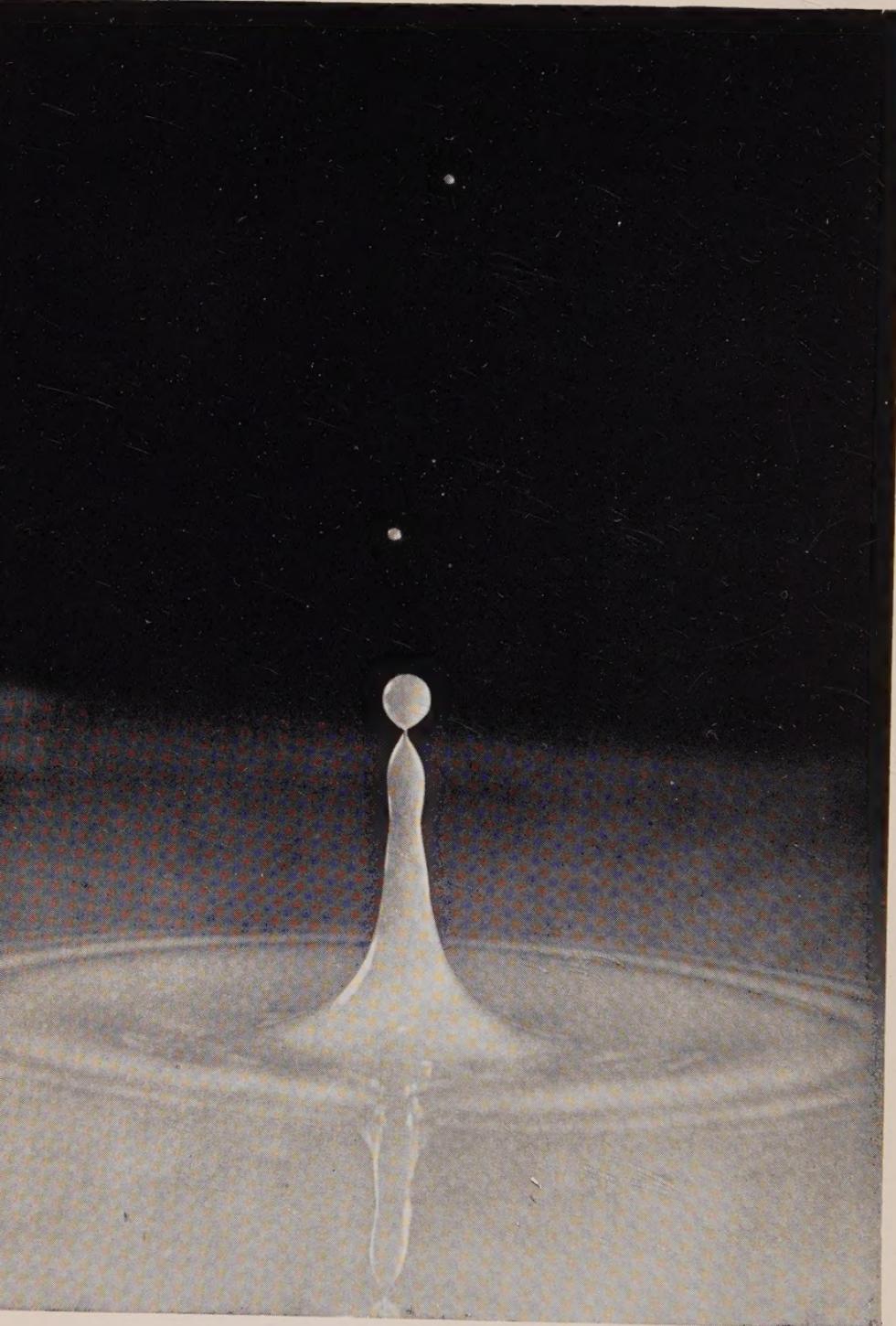
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GROWTH AND FORM



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latter phase of a splash: the crater has subsided, a columnar jet has risen up, and the jet is dividing into droplets. From Harold E. Edgerton, Massachusetts Technical Institution

ON
GROWTH AND FORM

BY
D'ARCY WENTWORTH THOMPSON

VOLUME I

Second edition, reprinted

Cambridge
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PREFATORY NOTE

THIS book of mine has little need of preface, for indeed it is "all preface" from beginning to end. I have written it as an easy introduction to the study of organic Form, by methods which are the common-places of physical science, which are by no means novel in their application to natural history, but which nevertheless naturalists are little accustomed to employ.

It is not the biologist with an inkling of mathematics, but the skilled and learned mathematician who must ultimately deal with such problems as are sketched and adumbrated here. I pretend to no mathematical skill, but I have made what use I could of what tools I had; I have dealt with simple cases, and the mathematical methods which I have introduced are of the easiest and simplest kind. Elementary as they are, my book has not been written without the help—the indispensable help—of many friends. Like Mr Pope translating Homer, when I felt myself deficient I sought assistance! And the experience which Johnson attributed to Pope has been mine also, that men of learning did not refuse to help me.

I wrote this book in wartime, and its revision has employed me during another war. It gave me solace and occupation, when service was debarred me by my years.

Few are left of the friends who helped me write it, but I do not forget the debt I owe them all. Let me add another to these kindly names, that of Dr G. T. Bennett, of Emmanuel College, Cambridge; he has never wearied of collaboration with me, and his criticisms have been an education to receive.

D. W. T.

1916–1941.

“The reasonings about the wonderful and intricate operations of Nature are so full of uncertainty, that, as the Wise-man truly observes, *hardly do we guess aright at the things that are upon earth, and with labour do we find the things that are before us.*”
Stephen Hales, *Vegetable Staticks* (1727), p. 318, 1738.

“Ever since I have been enquiring into the works of Nature I have always loved and admired the Simplicity of her Ways.”
Dr George Martine (a pupil of Boerhaave’s), in *Medical Essays and Observations*, Edinburgh, 1747.

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A Splash of Milk	Frontispiece
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"The mathematicians are well acquainted with the difference between pure science, which has to do only with ideas, and the application of its laws to the use of life, in which they are constrained to submit to the imperfections of matter and the influence of accident." Dr Johnson, in the fourteenth *Rambler*, May 5, 1750.

"Natural History...is either the beginning or the end of physical science." Sir John Herschel, in *The Study of Natural Philosophy*, p. 221, 1831.

"I believe the day must come when the biologist will—without being a mathematician—not hesitate to use mathematical analysis when he requires it." Karl Pearson, in *Nature*, January 17, 1901.

CHAPTER I

INTRODUCTQRY

OF the chemistry of his day and generation, Kant declared that it was a science, but not Science—*eine Wissenschaft, aber nicht Wissenschaft*—for that the criterion of true science lay in its relation to mathematics*. This was an old story: for Roger Bacon had called mathematics *porta et clavis scientiarum*, and Leonardo da Vinci had said much the same†. Once again, a hundred years after Kant, Du Bois Reymond, profound student of the many sciences on which physiology is based, recalled the old saying, and declared that chemistry would only reach the rank of science, in the high and strict sense, when it should be found possible to explain chemical reactions in the light of their causal relations to the velocities, tensions and conditions of equilibrium of the constituent molecules; that, in short, the chemistry of the future must deal with molecular mechanics by the methods and in the strict language of mathematics, as the astronomy of Newton and Laplace dealt with the stars in their courses. We know how great a step was made towards this distant goal as Kant defined it, when van't Hoff laid the firm foundations of a mathematical chemistry, and earned his proud epitaph—*Physicam chemiae adiunxit*‡.

We need not wait for the full realisation of Kant's desire, to apply to the natural sciences the principle which he laid down. Though chemistry fall short of its ultimate goal in mathematical mechanics§, nevertheless physiology is vastly strengthened and enlarged by

* “Ich behaupte nur dass in jeder besonderen Naturlehre nur so viel eigentliche Wissenschaft angetroffen könne als darin Mathematik anzutreffen ist”: *Gesammelte Schriften*, IV, p. 470.

† “Nessuna humana investigazione si può dimandare vera scienzia s’essa non passa per le matematiche dimostrazione.”

‡ Cf. also Crum Brown, On an application of Mathematics to Chemistry, *Trans. R.S.E.* xxiv, pp. 691–700, 1867.

§ Ultimate, for, as Francis Bacon tells us: *Mathesis philosophiam naturalem terminare debet, non generare aut procreare.*

making use of the chemistry, and of the physics, of the age. Little by little it draws nearer to our conception of a true science with each branch of physical science which it brings into relation with itself: with every physical law and mathematical theorem which it learns to take into its employ*. Between the physiology of Haller, fine as it was, and that of Liebig, Helmholtz, Ludwig, Claude Bernard, there was all the difference in the world†.

As soon as we adventure on the paths of the physicist, we learn to *weigh* and to *measure*, to deal with time and space and mass and their related concepts, and to find more and more our knowledge expressed and our needs satisfied through the concept of *number*, as in the dreams and visions of Plato and Pythagoras; for modern chemistry would have gladdened the hearts of those great philosophic dreamers. Dreams apart, numerical precision is the very soul of science, and its attainment affords the best, perhaps the only criterion of the truth of theories and the correctness of experiments‡. So said Sir John Herschel, a hundred years ago; and Kant had said that it was Nature herself, and not the mathematician, who brings mathematics into natural philosophy.

But the zoologist or morphologist has been slow, where the physiologist has long been eager, to invoke the aid of the physical or mathematical sciences; and the reasons for this difference lie deep, and are partly rooted in old tradition and partly in the diverse minds and temperaments of men. To treat the living body as a mechanism was repugnant, and seemed even ludicrous, to Pascal§; and Goethe, lover of nature as he was, ruled mathematics out of place in natural history. Even now the zoologist has scarce begun to dream of defining in mathematical language even the simplest organic forms. When he meets with a simple geometrical

* "Sine profunda Mechanics Scientia nil veri vos intellecturos, nil boni prolaturos alius": Boerhaave, *De usu ratiocinii Mechanici in Medicina*, 1713.

† It is well within my own memory how Thomson and Tait, and Klein and Sylvester had to lay stress on the mathematical aspect, and urge the mathematical study, of physical science itself!

‡ Dr Johnson says that "to count is a modern practice, the ancient method was to guess"; but Seneca was alive to the difference—"magnum esse solem philosophus probabit, quantus sit mathematicus."

§ Cf. *Pensées*, xxix, "Il faut dire, en gros, celà se fait par figure et mouvement, car celà est vrai. Mais de dire quels, et composer la machine, celà est ridicule, car celà est inutile, et incertain, et pénible."

construction, for instance in the honeycomb, he would fain refer it to psychical instinct, or to skill and ingenuity, rather than to the operation of physical forces or mathematical laws; when he sees in snail, or nautilus, or tiny foraminiferal or radiolarian shell a close approach to sphere or spiral, he is prone of old habit to believe that after all it is something more than a spiral or a sphere, and that in this "something more" there lies what neither mathematics nor physics can explain. In short, he is deeply reluctant to compare the living with the dead, or to explain by geometry or by mechanics the things which have their part in the mystery of life. Moreover he is little inclined to feel the need of such explanations, or of such extension of his field of thought. He is not without some justification if he feels that in admiration of nature's handiwork he has an horizon open before his eyes as wide as any man requires. He has the help of many fascinating theories within the bounds of his own science, which, though a little lacking in precision, serve the purpose of ordering his thoughts and of suggesting new objects of enquiry. His art of classification becomes an endless search after the blood-relationships of things living and the pedigrees of things dead and gone. The facts of embryology record for him (as Wolff, von Baer and Fritz Müller proclaimed) not only the life-history of the individual but the ancient annals of its race. The facts of geographical distribution or even of the migration of birds lead on and on to speculations regarding lost continents, sunken islands, or bridges across ancient seas. Every nesting bird, every ant-hill or spider's web, displays its psychological problems of instinct or intelligence. Above all, in things both great and small, the naturalist is rightfully impressed and finally engrossed by the peculiar beauty which is manifested in apparent fitness or "adaptation"—the flower for the bee, the berry for the bird.

Some lofty concepts, like space and number, involve truths remote from the category of causation; and here we must be content, as Aristotle says, if the mere facts be known*. But natural history deals with ephemeral and accidental, not eternal nor universal

* οὐδὲ ἀπαιτητέον δ' οὐδὲ τὴν αἰτίαν ὁμοίως, ἀλλ' ἵκανὸν Εν τισι τὸ δτι δειχθῆναι καλῶς Eth. Nic. 1098a, 33. Teleologist as he was at heart, Aristotle realised that mathematics was on another plane to teleology: τὰς δὲ μαθηματικὰς οὐθένα ποιεῖσθαι λόγον περὶ ἀγαθῶν καὶ κακῶν. Met. 996a, 35.

things; their causes and effects thrust themselves on our curiosity, and become the ultimate relations to which our contemplation extends*.

Time out of mind it has been by way of the "final cause," by the teleological concept of end, of purpose or of "design," in one of its many forms (for its moods are many), that men have been chiefly wont to explain the phenomena of the living world; and it will be so while men have eyes to see and ears to hear withal. With Galen, as with Aristotle†, it was the physician's way; with John Ray‡, as with Aristotle, it was the naturalist's way; with Kant, as with Aristotle, it was the philosopher's way. It was the old Hebrew way, and has its splendid setting in the story that God made "every plant of the field before it was in the earth, and every herb of the field before it grew." It is a common way, and a great way; for it brings with it a glimpse of a great vision, and it lies deep as the love of nature in the hearts of men.

The argument of the final cause is conspicuous in eighteenth-century physics, half overshadowing the "efficient" or physical cause in the hands of such men as Euler§, or Fermat or Maupertuis, to whom Leibniz|| had passed it on. Half overshadowed by the mechanical concept, it runs through Claude Bernard's *Leçons sur les phénomènes de la Vie¶*, and abides in much of modern physiology**.

* "All reasonings concerning matters of fact seem to be founded on the relation of Cause and Effect. By means of that relation alone we go beyond the evidence of our memory and senses": David Hume, *On the Operations of the Understanding*.

† E.g. "In the works of Nature *purpose*, not accident, is the main thing": τὸ γὰρ μὴ τυχόντως, ἀλλ᾽ ἐνεκά τίνος, ἐν τοῖς τῆς φύσεως ἔργοις ἐστὶ καὶ μάλιστα. *PA*, 645a, 24.

‡ E.g. "Quaeri fortasse a nonnullis potest, Quis Papilionum usus? Respondeo, ad ornatum Universi, et ut hominibus spectaculo sint." Joh. Raii, *Hist. Insectorum*, p. 109.

§ "Quum enim Mundi universi fabrica sit perfectissima, atque a Creatore sapientissimo absoluta, nihil omnino in Mundo contingit in quo non maximi minimi ratio quaepiam eluceat; quamobrem dubium prorsus est nullum quin omnes Mundi effectus ex causis finalibus, ope Methodi maximorum et minimorum, aequo feliciter determinari queant atque ex ipsis causis efficientibus." *Methodus inveniendi*, etc., 1744, p. 245 (*cit. Mach, Science of Mechanics*, 1902, p. 455).

|| Cf. *Opera* (ed. Erdmann), p. 106, "Bien loin d'exclure les causes finales... c'est de là qu'il faut tout déduire en Physique": in sharp contrast to Descartes's teaching, "Nullas unquam res naturales à fine, quem Deus aut Natura in iis faciendis sibi iproposuit, desumemus, etc." *Princip. I*, 28.

¶ Cf. p. 162. "La force vitale dirige des phénomènes qu'elle ne produit pas: les agents physiques produisent des phénomènes qu'ils ne dirigent pas."

** It is now and then conceded with reluctance. Thus Paolo Enriques, a learned and philosophic naturalist, writing "dell' economia di sostanza nelle osse cave"

Inherited from Hegel, it dominated Oken's *Naturphilosophie* and lingered among his later disciples, who were wont to liken the course of organic evolution not to the straggling branches of a tree, but to the building of a temple, divinely planned, and the crowning of it with its polished minarets*.

It is retained, somewhat crudely, in modern embryology, by those who see in the early processes of growth a significance "rather prospective than retrospective," such that the embryonic phenomena must "be referred directly to their usefulness in building up the body of the future animal†":—which is no more, and no less, than to say, with Aristotle, that the organism is the *τέλος*, or final cause, of its own processes of generation and development. It is writ large in that Entelechy‡ which Driesch rediscovéred, and which he made known to many who had neither learned of it from Aristotle, nor studied it with Leibniz, nor laughed at it with Rabelais and Voltaire. And, though it is in a very curious way, we are told that teleology was "refounded, reformed and rehabilitated" by Darwin's concept of the origin of species§; for, just as the older naturalists held (as Addison|| puts it) that "the make of every kind of animal is different from that of every other kind; and yet there is not the least turn in the muscles, or twist in the fibres of any one, which does not render them more proper for that particular animal's way of life than any other cut or texture of them would have been": so, by the theory of natural selection, "every variety of form and colour was urgently and absolutely called upon to produce its title

(*Arch. f. Entw. Mech.* xx, 1906), says "una certa impronta di teleologismo quale là è rimasta, mio malgrado, in questo scritto."

* Cf. John Cleland, On terminal forms of life, *Journ. Anat. and Physiol.* xviii, 1884.

† Conklin, Embryology of *Crepidula*, *Journ. of Morphol.* xiii, p. 203, 1897; cf. F. R. Lillie, Adaptation in cleavage, *Wood's Hole Biol. Lectures*, 1899, pp. 43–67.

‡ I am inclined to trace back Driesch's teaching of Entelechy to no less a person than Melanchthon. When Bacon (*de Augm.* iv, 3) states with disapproval that the soul "has been regarded rather as a function than as a substance," Leslie Ellis points out that he is referring to Melanchthon's exposition of the Aristotelian doctrine. For Melanchthon, whose view of the peripatetic philosophy had great and lasting influence in the Protestant Universities, affirmed that, according to the true view of Aristotle's opinion, the soul is not a substance but an *έντελέχεια*, or *function*. He defined it as *δύναμις quaedam ciens actiones*—a description all but identical with that of Claude Bernard's "*force vitale*."

§ Ray Lankester, art. Zoology, *Encycl. Brit.* (9th edit.), 1888, p. 806.

|| *Spectator*, No. 120.

to existence either as an active useful agent, or as a "survival" of such active usefulness in the past. But in this last, and very important case, we have reached a teleology without a *τέλος*, as men like Butler and Janet have been prompt to shew, an "adaptation" without "design," a teleology in which the final cause becomes little more, if anything, than the mere expression or resultant of a sifting out of the good from the bad, or of the better from the worse, in short of a process of mechanism. The apparent manifestations of purpose or adaptation become part of a mechanical philosophy, "une forme méthodologique de connaissance*," according to which "la Nature agit toujours par les moyens les plus simples†," and "chaque chose finit toujours par s'accommoder à son milieu," as in the Epicurean creed or aphorism that Nature *finds a use* for everything‡. In short, by a road which resembles but is not the same as Maupertuis's road, we find our way to the very world in which we are living, and find that, if it be not, it is ever tending to become, "the best of all possible worlds§."

But the use of the teleological principle is but one way, not the whole or the only way, by which we may seek to learn how things came to be, and to take their places in the harmonious complexity of the world. To seek not for ends but for antecedents is the way of the physicist, who finds "causes" in what he has learned to recognise as fundamental properties, or inseparable concomitants, or unchanging laws, of matter and of energy. In Aristotle's parable, the house is there that men may live in it; but it is also there because the builders have laid one stone upon another. It is as a *mechanism*, or a mechanical construction, that the physicist looks upon the world; and Democritus, first of physicists and one of the greatest of the Greeks, chose to refer all natural phenomena to mechanism and set the final cause aside.

* So Newton, in the Preface to the *Principia*: "Natura enim simplex est, et rerum causis superfluis non luxuriat"; "Nature is pleased with simplicity, and affects not the pomp of superfluous causes." Modern physics finds the perfection of mathematical beauty in what Newton called the perfection of simplicity.

† Janet, *Les Causes Finales*, 1876, p. 350.

‡ "Nil ideo quoniam natumst in corpore uti Possemus sed quod natumst id procreat usum." Lucret. iv, 834.

§ The phrase is Leibniz's, in his *Théodicée*: and harks back to Aristotle—If one way be better than another, that you may be sure is Nature's way; *Nic. Eth.* 1099b, 23 *et al.*

Still, all the while, like warp and woof, mechanism and teleology are interwoven together, and we must not cleave to the one nor despise the other; for their union is rooted in the very nature of totality. We may grow shy or weary of looking to a final cause for an explanation of our phenomena; but after we have accounted for these on the plainest principles of mechanical causation it may be useful and appropriate to see how the final cause would tally with the other, and lead towards the same conclusion*. Maupertuis had little liking for the final cause, and shewed some sympathy with Descartes in his repugnance to its application to physical science. But he found at last, taking the final and the efficient causes one with another, that “l’harmonie de ces deux attributs est si parfaite que sans doute tous les effets de la Nature se pourroient déduire de chacun pris séparément. Une Mécanique aveugle et nécessaire suit les dessins de l’Intelligence la plus éclairée et la plus libre†.” Boyle also, the Father of Chemistry, wrote, in his latter years, a *Disquisition about the Final Causes of Natural Things: Wherein it is Inquir’d Whether, And (if at all) With what Cautions, a Naturalist should admit Them?* He found “that all consideration of final cause is not to be banished from Natural Philosophy...”; but on the other hand “that the naturalist who would deserve that name must not let the search and knowledge of final causes make him neglect the industrious indagation of efficient‡.” In our own day the philosopher neither minimises nor unduly magnifies the mechanical aspect of the Cosmos; nor need the naturalist either exaggerate or belittle the mechanical phenomena which are profoundly associated with Life, and inseparable from our understanding of Growth and Form.

* “S’il est dangereux de se servir des causes finales à priori pour trouver les lois des phénomènes, il est peut-être utile et il est au moins curieux de faire voir comment le principe des causes finales s'accorde avec les lois des phénomènes, pourvu qu'on commence par déterminer ces lois d'après les principes de mécanique clairs et incontestables.” (D'Alembert, Art. Causes finales, *Encyclopédie*, II, p. 789, 1751.)

† See his essay on the “*Accord des différentes lois de la Nature.*”

‡ Cf. also Leibniz (*Discours de la Métaphysique: Lettres inédites*, ed. de Careil, 1857, p. 354), “L’un et l’autre est bon, l’un et l’autre peut être utile...et les auteurs qui suivent ces deux routes différentes ne devraient pas se maltraiter.” Or again in the *Monadologie*, “Les âmes agissent selon les causes finales...Les corps agissent selon les lois des causes efficientes ou des mouvements. Et les deux règnes, celui des causes efficientes et des causes finales sont harmonieux entre eux.”

Nevertheless, when philosophy bids us hearken and obey the lessons both of mechanical and of teleological interpretation, the precept is hard to follow: so that oftentimes it has come to pass, just as in Bacon's day, that a leaning to the side of the final cause "hath intercepted the severe and diligent enquiry of all real and physical causes," and has brought it about that "the search of the physical cause hath been neglected and passed in silence." So long and so far as "fortuitous variation*" and the "survival of the fittest" remain engrained as fundamental and satisfactory hypotheses in the philosophy of biology, so long will these "satisfactory and specious causes" tend to stay "severe and diligent enquiry... to the great arrest and prejudice of future discovery." Long before the great Lord Keeper wrote these words, Roger Bacon had shewn how easy it is, and how vain, to survey the operations of Nature and idly refer her wondrous works to chance or accident, or to the immediate interposition of God†.

The difficulties which surround the concept of ultimate or "real" causation, in Bacon's or Newton's sense of the word, the insuperable difficulty of giving any just and tenable account of the relation of cause and effect from the empirical point of view, need scarcely hinder us in our physical enquiry. As students of mathematical and experimental physics we are content to deal with those antecedents, or concomitants, of our phenomena without which the phenomenon does not occur—with causes, in short, which, *aliae ex aliis aptae et necessitate nexae*, are no more, and no less, than conditions *sine qua non*. Our purpose is still adequately fulfilled: inasmuch as we are still enabled to correlate, and to equate, our particular phenomena with more and more of the physical phenomena around, and so to weave a web of connection and interdependence which shall serve our turn, though the metaphysician withhold from that interdependence the title of causality‡. We come in touch

* The reader will understand that I speak, not of the "severe and diligent enquiry" of variation or of fortuity, but merely of the easy assumption that these phenomena are a sufficient basis on which to rest, with the all-powerful help of natural selection, a theory of definite and progressive evolution.

† *Op. tert.* (ed. Brewer, p. 99). "Ideo mirabiles actiones naturae, quae tota die fiunt in nobis et in rebus coram oculis nostris, non percipimus; sed aestimamus eas fieri vel per specialem operationem divinam... vel à casu et fortuna."

‡ Cf. Fourier's phrase, in his *Théorie de la Chaleur*, with which Thomson and Tait prefaced their *Treatise on Natural Philosophy*: "Les causes primordiales ne

with what the schoolmen called a *ratio cognoscendi*, though the true *ratio efficiendi* is still enwrapped in many mysteries. And so handled, the quest of physical causes merges with another great Aristotelian theme—the search for relations between things apparently disconnected, and for “similitude in things to common view unlike*.” Newton did not shew the cause of the apple falling, but he shewed a similitude (“the more to increase our wonder, with an apple”) between the apple and the stars†. By doing so he turned old facts into new knowledge; and was well content if he could bring diverse phenomena under “two or three Principles of Motion” even “though the Causes of these Principles were not yet discovered”.

Moreover, the naturalist and the physicist will continue to speak of “causes”, just as of old, though it may be with some mental reservations: for, as a French philosopher said in a kindred difficulty: “ce sont là des manières de s’exprimer, et si elles sont interdites il faut renoncer à parler de ces choses.”

The search for differences or fundamental contrasts between the phenomena of organic and inorganic, of animate and inanimate, things, has occupied many men’s minds, while the search for community of principles or essential similitudes has been pursued by few; and the contrasts are apt to loom too large, great though they may be. M. Dunan, discussing the *Problème de la Vie*‡, in an essay which M. Bergson greatly commends, declares that “les lois physico-chimiques sont aveugles et brutales; là où elles règnent seules, au lieu d’un ordre et d’un concert, il ne peut y avoir qu’incohérence et chaos.” But the physicist proclaims aloud that the physical phenomena which meet us by the way have their forms not less beautiful and scarce less varied than those which move us to admiration: “mais elles sont assujetties à des lois simples et constantes, que l’on peut découvrir par l’observation, et dont l’étude est l’objet de la philosophie naturelle.”

* “Plurimum amo analogias, fidelissimos meos magistros, omnium Naturae arcanorum conscos,” said Kepler; and Perrin speaks with admiration, in *Les Atomes*, of men like Galileo and Carnot, who “possessed the power of perceiving analogies to an extraordinary degree.” Hume declared, and Mill said much the same thing, that all reasoning whatsoever depends on resemblance or analogy, and the power to recognise it. Comparative anatomy (as Vicq d’Azyr first called it), or comparative physics (to use a phrase of Mach’s), are particular instances of a sustained search for analogy or similitude.

† As for Newton’s apple, see De Morgan, in *Notes and Queries* (2), vi, p. 169, 1858.

‡ *Revue Philosophique*, xxxiii, 1892.

tion among living things. The waves of the sea, the little ripples on the shore, the sweeping curve of the sandy bay between the headlands, the outline of the hills, the shape of the clouds, all these are so many riddles of form, so many problems of morphology, and all of them the physicist can more or less easily read and adequately solve: solving them by reference to their antecedent phenomena, in the material system of mechanical forces to which they belong, and to which we interpret them as being due. They have also, doubtless, their *immanent* teleological significance; but it is on another plane of thought from the physicist's that we contemplate their intrinsic harmony* and perfection, and "see that they are good."

Nor is it otherwise with the material forms of living things. Cell and tissue, shell and bone, leaf and flower, are so many portions of matter, and it is in obedience to the laws of physics that their particles have been moved, moulded and conformed†. They are no exception to the rule that Θεὸς ἀεὶ γεωμετρεῖ. Their problems of form are in the first instance mathematical problems, their problems of growth are essentially physical problems, and the morphologist is, *ipso facto*, a student of physical science. He may learn from that comprehensive science, as the physiologists have not failed to do, the point of view from which her problems are approached, the quantitative methods by which they are attacked, and the wholesome restraints under which all her work is done. He may come to realise that there is no branch of mathematics, however abstract, which may not some day be applied to phenomena of the real

* What I understand by "holism" is what the Greeks called *άρμονία*. This is something exhibited not only by a lyre in tune, but by all the handiwork of craftsmen, and by all that is "put together" by art or nature. It is the "compositeness of any composite whole"; and, like the cognate terms *κράσις* or *σύνθεσις*, implies a balance or attunement. Cf. John Tate, in *Class. Review*, Feb. 1939.

† This general principle was clearly grasped by Mr George Rainey many years ago, and expressed in such words as the following: "It is illogical to suppose that in the case of vital organisms a distinct force exists to produce results perfectly within the reach of physical agencies, especially as in many instances no end could be attained were that the case, but that of opposing one force by another capable of effecting exactly the same purpose." (On artificial calculi, *Q.J.M.S.* (*Trans. Microsc. Soc.*), vi, p. 49, 1858.) Cf. also Helmholtz, *infra cit.* p. 9. (Mr George Rainey, a man of learning and originality, was demonstrator of anatomy at St Thomas's; he followed that modest calling to a great age, and is remembered by a few old pupils with peculiar affection.)

world*. He may even find a certain analogy between the slow, reluctant extension of physical laws to vital phenomena and the slow triumphant demonstration by Tycho Brahé, Copernicus, Galileo and Newton (all in opposition to the Aristotelian cosmogony), that the heavens are formed of like substance with the earth, and that the movements of both are subject to the selfsame laws.

Organic evolution has its physical analogue in the universal law that the world tends, in all its parts and particles, to pass from certain less probable to certain more probable configurations or states. This is the second law of thermodynamics. It has been called *the law of evolution of the world†*; and we call it, after Clausius, the Principle of *Entropy*, which is a literal translation of *Evolution* into Greek.

The introduction of mathematical concepts into natural science has seemed to many men no mere stumbling-block, but a very parting of the ways. Bichat was a man of genius, who did immense service to philosophical anatomy, but, like Pascal, he utterly refused to bring physics or mathematics into biology: “On calcule le retour d’un comète, les résistances d’un fluide parcourant un canal inerte, la vitesse d’un projectile, etc.; mais calculer avec Borelli la force d’un muscle, avec Keil la vitesse du sang, avec Jurine, Lavoisier et d’autres la quantité d’air entrant dans le poumon, c’est bâtir sur un sable mouvant un édifice solide par lui-même, mais qui tombe bientôt faute de base assurée‡.” Comte went further still, and said that every attempt to introduce mathematics into chemistry must be deemed profoundly irrational, and contrary to the whole spirit of the science§. But the great makers of modern science have all gone the other way. Von Baer, using a bold metaphor, thought that it might become possible “die bildenden Kräfte des thierischen Körpers auf die allgemeinen Kräfte oder *Lebenserscheinungen des Weltganzen* zurückzuführen||.” Thomas Young shewed, as Borelli had done, how physics may subserve anatomy; he learned from the heart and arteries that “the mechanical motions which take place in an animal’s body are regulated by the same general laws as the motions of

* So said Lobatchevsky.

† Cf. Chwolson, *Lehrbuch*, III, p. 499, 1905; J. Perrin, *Traité de chimie physique*, I, p. 142, 1903; and Lotka’s *Elements of Physical Biology*, 1925, p. 26.

‡ *La Vie et la Mort*, p. 81.

§ *Philosophie Positive*, Bk. IV.

|| Ueber Entwicklung der Thiere: Beobachtungen und Reflexionen, I, p. 22, 1828.

inanimate bodies*.” And Theodore Schwann said plainly, a hundred years ago, “Ich wiederhole übrigens dass, wenn hier von einer physikalischen Erklärung der organischen Erscheinungen die Rede ist, darunter nicht nothwendig eine Erklärung durch die bekannten physikalischen Kräfte... zu verstehen ist, sondern überhaupt eine Erklärung durch Kräfte, die nach strengen Gesetzen der blinden Nothwendigkeit wie die physikalischen Kräfte wirken, mögen diese Kräfte auch in der anorganischen Natur auftreten oder nicht†.”

Helmholtz, in a famous and influential lecture, and surely with these very words of Schwann’s in mind, laid it down as the fundamental principle of physiology that “there may be other agents acting in the living body than those agents which act in the inorganic world; but these forces, so far as they cause chemical and mechanical influence in the body, must be *quite of the same character* as inorganic forces: in this, at least, that their effects must be ruled by necessity, and must always be the same when acting under the same conditions; and so there cannot exist any arbitrary choice in the direction of their actions.” It follows further that, like the other “physical” forces, they must be subject to mathematical analysis and deduction‡.

So much for the physico-chemical problems of physiology. Apart from these, the road of physico-mathematical or dynamical investigation in morphology has found few to follow it; but the pathway is old. The way of the old Ionian physicians, of Anaxagoras§, of Empedocles and his disciples in the days before Aristotle, lay just by that highway side. It was Galileo’s and Borelli’s way; and Harvey’s way, when he discovered the circulation of the blood||. It was little trodden for long afterwards, but once in a while Swammerdam and Réaumur passed thereby. And of later years Moseley and Meyer, Berthold, Errera and Roux have been among

* Croonian Lecture on the heart and arteries, *Phil. Trans.* 1809, p. 1; *Collected Works*, I, p. 511.

† *Mikroskopische Untersuchungen*, 1839, p. 226.

‡ The conservation of forces applied to organic nature, *Proc. Royal Inst.* April 12, 1861.

§ Whereby he incurred the reproach of Socrates, in the *Phaedo*. See Clerk Maxwell on Anaxagoras as a Physicist, in *Phil. Mag.* (4), XLVI, pp. 453–460, 1873.

|| Cf. Harvey’s preface to his *Exercitationes de Generatione Animalium*, 1651: “Quoniam igitur in Generatione animalium (ut etiam in caeteris rebus omnibus de quibus aliquid scire cupimus), *inquisitio omnis à caussis petenda est, praesertim à materiali et efficiente: visum est mihi*” etc.

the little band of travellers. We need not wonder if the way be hard to follow, and if these wayfarers have yet gathered little. A harvest has been reaped by others, and the gleaning of the grapes is slow.

It behoves us always to remember that in physics it has taken great men to discover simple things. They are very great names indeed which we couple with the explanation of the path of a stone, the droop of a chain, the tints of a bubble, the shadows in a cup. It is but the slightest adumbration of a dynamical morphology that we can hope to have until the physicist and the mathematician shall have made these problems of ours their own, or till a new Boscovich shall have written for the naturalist the new *Theoria Philosophiae Naturalis*.

How far even then mathematics will suffice to describe, and physics to explain, the fabric of the body, no man can foresee. It may be that all the laws of energy, and all the properties of matter, and all the chemistry of all the colloids are as powerless to explain the body as they are impotent to comprehend the soul. For my part, I think it is not so. Of how it is that the soul informs the body, physical science teaches me nothing; and that living matter influences and is influenced by mind is a mystery without a clue. Consciousness is not explained to my comprehension by all the nerve-paths and neurones of the physiologist; nor do I ask of physics how goodness shines in one man's face, and evil betrays itself in another. But of the construction and growth and working of the body, as of all else that is of the earth earthly, physical science is, in my humble opinion, our only teacher and guide.

Often and often it happens that our physical knowledge is inadequate to explain the mechanical working of the organism; the phenomena are superlatively complex, the procedure is involved and entangled, and the investigation has occupied but a few short lives of men. When physical science falls short of explaining the order which reigns throughout these manifold phenomena—an order more characteristic in its totality than any of its phenomena in themselves—men hasten to invoke a guiding principle, an entelechy, or call it what you will. But all the while no physical law, any more than gravity itself, not even among the puzzles of stereo-chemistry or of physiological surface-action and osmosis, is known to be transgressed by the bodily mechanism.

Some physicists declare, as Maxwell did, that atoms or molecules more complicated by far than the chemist's hypotheses demand, are requisite to explain the phenomena of life. If what is implied be an explanation of psychical phenomena, let the point be granted at once; we may go yet further and decline, with Maxwell, to believe that anything of the nature of physical complexity, however exalted, could ever suffice. Other physicists, like Auerbach*, or Larmor†, or Joly‡, assure us that our laws of thermodynamics do not suffice, or are inappropriate, to explain the maintenance, or (in Joly's phrase) the accelerative absorption, of the bodily energies, the retardation of entropy, and the long battle against the cold and darkness which is death. With these weighty problems I am not for the moment concerned. My sole purpose is to correlate with mathematical statement and physical law certain of the simpler outward phenomena of organic growth and structure or form, while all the while regarding the fabric of the organism, *ex hypothesi*, as a material and mechanical configuration. This is my purpose here. But I would not for the world be thought to believe that this is the only story which Life and her Children have to tell. One does not come by studying living things for a lifetime to suppose that physics and chemistry can account for them all§.

Physical science and philosophy stand side by side, and one upholds the other. Without something of the strength of physics philosophy would be weak; and without something of philosophy's wealth physical science would be poor. "Rien ne retirera du tissu de la science les fils d'or que la main du philosophe y a introduits||." But there are fields where each, for a while at least, must work alone; and where physical science reaches its limitations physical science itself must help us to discover. Meanwhile the appropriate and

* *Ektropismus, oder die physikalische Theorie des Lebens*, Leipzig, 1810.

† Wilde Lecture, *Nature*, March 12, 1908; *ibid.* Sept. 6, 1900; *Aether and Matter*, p. 288. Cf. also Kelvin, *Fortnightly Review*, 1892, p. 313.

‡ The abundance of life, *Proc. Roy. Dublin Soc.* vii, 1890; *Scientific Essays*, 1915, p. 60 seq.

§ That mechanism has its share in the scheme of nature no philosopher has denied. Aristotle (or whosoever wrote the *De Mundo*) goes so far as to assert that in the most mechanical operations of nature we behold some of the divinest attributes of God.

|| J. H. Fr. Papillon, *Histoire de la philosophie moderne dans ses rapports avec le développement des sciences de la nature*, I, p. 300, 1876.

legitimate postulate of the physicist, in approaching the physical problems of the living body, is that with these physical phenomena no alien influence interferes. But the postulate, though it is certainly legitimate, and though it is the proper and necessary prelude to scientific enquiry, may some day be proven to be untrue; and its disproof will not be to the physicist's confusion, but will come as his reward. In dealing with forms which are so concomitant with life that they are seemingly controlled by life, it is in no spirit of arrogant assertiveness if the physicist begins his argument, after the fashion of a most illustrious exemplar, with the old formula of scholastic challenge: *An Vita sit? Dico quod non.*

The terms Growth and Form, which make up the title of this book, are to be understood, as I need hardly say, in their relation to the study of organisms. We want to see how, in some cases at least, the forms of living things, and of the parts of living things, can be explained by physical considerations, and to realise that in general no organic forms exist save such as are in conformity with physical and mathematical laws. And while growth is a somewhat vague word for a very complex matter, which may depend on various things, from simple imbibition of water to the complicated results of the chemistry of nutrition, it deserves to be studied in relation to form: whether it proceed by simple increase of size without obvious alteration of form, or whether it so proceed as to bring about a gradual change of form and the slow development of a more or less complicated structure.

In the Newtonian language* of elementary physics, force is recognised by its action in producing or in changing motion, or in preventing change of motion or in maintaining rest. When we deal with matter in the concrete, force does not, strictly speaking, enter into the question, for force, unlike matter, has no independent objective existence. It is energy in its various forms, known or unknown, that acts upon matter. But when we abstract our thoughts from the material to its form, or from the thing moved to its motions, when we deal with the subjective conceptions of form,

* It is neither unnecessary nor superfluous to explain that physics is passing through an empirical phase into a phase of pure mathematical reasoning. But when we use physics to interpret and elucidate our biology, it is the old-fashioned empirical physics which we endeavour, and are alone able, to apply.

or movement, or the movements that change of form implies, then Force is the appropriate term for our conception of the causes by which these forms and changes of form are brought about. When we use the term force, we use it, as the physicist always does, for the sake of brevity, using a symbol for the magnitude and direction of an action in reference to the symbol or diagram of a material thing. It is a term as subjective and symbolic as form itself, and so is used appropriately in connection therewith.

The form, then, of any portion of matter, whether it be living or dead, and the changes of form which are apparent in its movements and in its growth, may in all cases alike be described as due to the action of force. In short, the form of an object is a "diagram of forces," in this sense, at least, that from it we can judge of or deduce the forces that are acting or have acted upon it: in this strict and particular sense, it is a diagram—in the case of a solid, of the forces which *have* been impressed upon it when its conformation was produced, together with those which enable it to retain its conformation; in the case of a liquid (or of a gas) of the forces which are for the moment acting on it to restrain or balance its own inherent mobility. In an organism, great or small, it is not merely the nature of the *motions* of the living substance which we must interpret in terms of force (according to kinetics), but also the *conformation* of the organism itself, whose permanence or equilibrium is explained by the interaction or balance of forces, as described in statics.

If we look at the living cell of an Amoeba or a Spirogyra, we see a something which exhibits certain active movements, and a certain fluctuating, or more or less lasting, form; and its form at a given moment, just like its motions, is to be investigated by the help of physical methods, and explained by the invocation of the mathematical conception of force.

Now the state, including the shape or form, of a portion of matter is the resultant of a number of forces, which represent or symbolise the manifestations of various kinds of energy; and it is obvious, accordingly, that a great part of physical science must be understood or taken for granted as the necessary preliminary to the discussion on which we are engaged. But we may at least try to indicate, very briefly, the nature of the principal forces and the

principal properties of matter with which our subject obliges us to deal. Let us imagine, for instance, the case of a so-called "simple" organism, such as Amoeba; and if our short list of its physical properties and conditions be helpful to our further discussion, we need not consider how far it be complete or adequate from the wider physical point of view*.

This portion of matter, then, is kept together by the inter-molecular force of cohesion; in the movements of its particles relatively to one another, and in its own movements relative to adjacent matter, it meets with the opposing force of friction—without the help of which its creeping movements could not be performed. It is acted on by gravity, and this force tends (though slightly, owing to the Amoeba's small mass, and to the small difference between its density and that of the surrounding fluid) to flatten it down upon the solid substance on which it may be creeping. Our Amoeba tends, in the next place, to be deformed by any pressure from outside, even though slight, which may be applied to it, and this circumstance shews it to consist of matter in a fluid, or at least semi-fluid, state: which state is further indicated when we observe streaming or current motions in its interior. Like other fluid bodies, its surface†, whatsoever other substance—gas, liquid or solid—it be in contact with, and in varying degree according to the nature of that adjacent substance, is the seat of molecular force exhibiting itself as a surface-tension, from the action of which many important consequences follow, greatly affecting the form of the fluid surface.

While the protoplasm‡ of the Amoeba reacts to the slightest pressure, and tends to "flow," and while we therefore speak of it

* With the special and important properties of *colloidal* matter we are, for the time being, not concerned.

† Whether an animal cell has a membrane, or only a pellicle or *zona limitans*, was once deemed of great importance, and played a big part in the early controversies between the cell-theory of Schwann and the protoplasma-theory of Max Schultze and others. Dujardin came near the truth when he said, somewhat naïvely, "en niant la présence d'un tégument propre, je ne prétends pas du tout nier l'existence d'une surface."

‡ The word protoplasm is used here in its most general sense, as vaguely as when Huxley spoke of it as the "physical basis of life." Its many changes and shades of meaning in early years are discussed by Van Bambeke in the *Bull. Soc. Belge de Microscopie*, xxii, pp. 1-16, 1896.

as a fluid*, it is evidently far less mobile than such a fluid (for instance) as water, but is rather like treacle in its slow creeping movements as it changes its shape in response to force. Such fluids are said to have a high viscosity, and this viscosity obviously acts in the way of resisting change of form, or in other words of retarding the effects of any disturbing action of force. When the viscous fluid is capable of being drawn out into fine threads, a property in which we know that some Amoebae differ greatly from others, we say that the fluid is also *viscid*, or exhibits viscosity. Again, not by virtue of our Amoeba being liquid, but at the same time in vastly greater measure than if it were a solid (though far less rapidly than if it were a gas), a process of molecular diffusion is constantly going on within its substance, by which its particles interchange their places within the mass, while surrounding fluids, gases and solids in solution diffuse into and out of it. In so far as the outer wall of the cell is different in character from the interior, whether it be a mere pellicle as in Amoeba or a firm cell-wall as in Protococcus, the diffusion which takes place *through* this wall is sometimes distinguished under the term *osmosis*.

Within the cell, chemical forces are at work, and so also in all probability (to judge by analogy) are electrical forces; and the organism reacts also to forces from without, that have their origin in chemical, electrical and thermal influences. The processes of diffusion and of chemical activity within the cell result, by the drawing in of water, salts, and food-material with or without chemical transformation into protoplasm, in *growth*, and this complex phenomenon we shall usually, without discussing its nature and origin, describe and picture as a *force*. Indeed we shall manifestly be inclined to use the term growth in two senses, just indeed as we do in the case of attraction or gravitation, on the one hand as a *process*, and on the other as a *force*.

In the phenomena of cell-division, in the attractions or repulsions of the parts of the dividing nucleus, and in the "caryokinetic" figures which appear in connection with it, we seem to see in operation forces and the effects of forces which have, to say the

* One of the first statements which Dujardin made about protoplasm (or, as he called it, *sarcode*) was that it was *not* a fluid; and he relied greatly on this fact to shew that it was a living, or an organised, structure.

least of it, a close analogy with known physical phenomena: and to this matter we shall presently return. But though they resemble known physical phenomena, their nature is still the subject of much dubiety and discussion, and neither the forms produced nor the forces at work can yet be satisfactorily and simply explained. We may readily admit then, that, besides phenomena which are obviously physical in their nature, there are actions visible as well as invisible taking place within living cells which our knowledge does not permit us to ascribe with certainty to any known physical force; and it may or may not be that these phenomena will yield in time to the methods of physical investigation. Whether they do or no, it is plain that we have no clear rule or guidance as to what is "vital" and what is not; the whole assemblage of so-called vital phenomena, or properties of the organism, cannot be clearly classified into those that are physical in origin and those that are *sui generis* and peculiar to living things. All we can do meanwhile is to analyse, bit by bit, those parts of the whole to which the ordinary laws of the physical forces more or less obviously and clearly and indubitably apply.

But even the ordinary laws of the physical forces are by no means simple and plain. In the winding up of a clock (so Kelvin once said), and in the properties of matter which it involves, there is enough and more than enough of mystery for our limited understanding: "a watchspring is much farther beyond our understanding than a gaseous nebula." We learn and learn, but never know all, about the smallest, humblest thing. So said St Bonaventure: "Si per multos annos viveres, adhuc naturam unius festucae seu muscae seu minimae creaturae de mundo ad plenum cognoscere non valeres*" There is a certain fascination in such ignorance; and we learn (like the Abbé Galiani) without discouragement that Science is "plutôt destiné à étudier qu'à connaître, à chercher qu'à trouver la vérité."

Morphology is not only a study of material things and of the forms of material things, but has its dynamical aspect, under which we deal with the interpretation, in terms of force, of the operations of Energy†. And here it is well worth while to remark that, in dealing

* Op. v, p. 541; cit. E. Gilson.

† This is a great theme. Boltzmann, writing in 1886 on the second law of thermodynamics, declared that available energy was the main object at stake in the struggle for existence and the evolution of the world. Cf. Lotka, The energetics of evolution, Proc. Nat. Acad. Sci. 1922, p. 147.

with the facts of embryology or the phenomena of inheritance, the common language of the books seems to deal too much with the *material* elements concerned, as the causes of development, of variation or of hereditary transmission. Matter as such produces nothing, changes nothing, does nothing; and however convenient it may afterwards be to abbreviate our nomenclature and our descriptions, we must most carefully realise in the outset that the spermatozoon, the nucleus, the chromosomes or the germ-plasma can never *act* as matter alone, but only as seats of energy and as centres of force. And this is but an adaptation (in the light, or rather in the conventional symbolism, of modern science) of the old saying of the philosopher: ἀρχὴ γὰρ ἡ φύσις μᾶλλον τῆς ὕλης.

Since this book was written, some five and twenty years ago, certain great physico-mathematical concepts have greatly changed. Newtonian mechanics and Newtonian concepts of space and time are found unsuitable, even untenable or invalid, for the all but infinitely great and the all but infinitely small. The very idea of physical causation is said to be illusory, and the physics of the atom and the electron, and of the quantum theory, are to be elucidated by the laws of probability rather than by the concept of causation and its effects. But the orders of magnitude, whether of space or time, within which these new concepts become useful, or hold true, lie far away. We distinguish, and can never help distinguishing, between the things which are of our own scale and order, to which our minds are accustomed and our senses attuned, and those remote phenomena which ordinary standards fail to measure, in regions where (as Robert Louis Stevenson said) there is no habitable city for the mind of man.

It is no wonder if new methods, new laws, new words, new modes of thought are needed when we make bold to contemplate a Universe within which all Newton's is but a speck. But the world of the living, wide as it may be, is bounded by a familiar horizon within which our thoughts and senses are at home, our scales of time and magnitude suffice, and the Natural Philosophy of Newton and Galileo rests secure.

We start, like Aristotle, with *our own* stock-in-trade of knowledge: ἀρκτέον ἀπὸ τῶν ἡμῖν γνωρίμων. And only when we are

steeped to the marrow (as Henri Poincaré once said) in the old laws, and in no danger of forgetting them, may we be allowed to learn how they have their remote but subtle limitations, and cease afar off to be more than approximately true*. Kant's axiom of causality, that it is *denknotwendig*—indispensable for thought—remains true however physical science may change. His later aphorism, that all changes take place subject to the law which links cause and effect together—"alle Veränderungen geschehen nach dem Gesetz der Verknüpfung von Ursache und Wirkung"—is still an axiom *à priori*, independent of experience: for experience itself depends upon its truth†.

* So Max Planck himself says somewhere: "In my opinion the teaching of mechanics will still have to begin with Newtonian force, just as optics begins in the sensation of colour and thermodynamics with the sensation of warmth, despite the fact that a more precise basis is substituted later on."

† "Weil er [der Grundsatz das Kausalverhältnisses] selbst der grund der Möglichkeit einer solchen Erfahrung ist": *Kritik d. reinen Vernunft*, ed. Odicke, 1889, p. 221. Cf. also G. W. Kellner, Die Kausalität in der Physik, *Ztschr. f. Physik*, LXIV, pp. 568–580, 1930.

CHAPTER II

ON MAGNITUDE

To terms of magnitude, and of direction, must we refer all our conceptions of Form. For the form of an object is defined when we know its magnitude, actual or relative, in various directions; and Growth involves the same concepts of magnitude and direction, related to the further concept, or “dimension,” of Time. Before we proceed to the consideration of specific form, it will be well to consider certain general phenomena of spatial magnitude, or of the extension of a body in the several dimensions of space.

We are taught by elementary mathematics—and by Archimedes himself—that in similar figures the surface increases as the square, and the volume as the cube, of the linear dimensions. If we take the simple case of a sphere, with radius r , the area of its surface is equal to $4\pi r^2$, and its volume to $\frac{4}{3}\pi r^3$; from which it follows that the ratio of its volume to surface, or V/S , is $\frac{1}{3}r$. That is to say, V/S varies as r ; or, in other words, the larger the sphere by so much the greater will be its volume (or its mass, if it be uniformly dense throughout) in comparison with its superficial area. And, taking L to represent any linear dimension, we may write the general equations in the form

$$S \propto L^2, \quad V \propto L^3,$$

or $S = kL^2$, and $V = k'L^3$,

where k, k' , are “factors of proportion,”

and $\frac{V}{S} \propto L$, or $\frac{V}{S} = \frac{k}{k'} L = KL$.

So, in Lilliput, “His Majesty’s Ministers, finding that Gulliver’s stature exceeded theirs in the proportion of twelve to one, concluded from the similarity of their bodies that his must contain at least 1728 [or 12^3] of theirs, and must needs be rationed accordingly*.”

* Likewise Gulliver had a whole Lilliputian hogshead for his half-pint of wine: in the due proportion of 1728 half-pints, or 108 gallons, equal to one pipe or

From these elementary principles a great many consequences follow, all more or less interesting, and some of them of great importance. In the first place, though growth in length (let us say) and growth in volume (which is usually tantamount to mass or weight) are parts of one and the same process or phenomenon, the one attracts our *attention* by its increase very much more than the other. For instance a fish, in doubling its length, multiplies its weight no less than eight times; and it all but doubles its weight in growing from four inches long to five.

In the second place, we see that an understanding of the correlation between length and weight in any particular species of animal, in other words a determination of k in the formula $W = k \cdot L^3$, enables us at any time to translate the one magnitude into the other, and (so to speak) to weigh the animal with a measuring-rod; this, however, being always subject to the condition that the animal shall in no way have altered its form, nor its specific gravity. That its specific gravity or density should materially or rapidly alter is not very likely; but as long as growth lasts changes of form, even though inappreciable to the eye, are apt and likely to occur. Now weighing is a far easier and far more accurate operation than measuring; and the measurements which would reveal slight and otherwise imperceptible changes in the form of a fish—slight relative differences between length, breadth and depth, for instance—would need to be very delicate indeed. But if we can make fairly accurate determinations of the length, which is much the easiest linear dimension to measure, and correlate it with the weight, then the value of k , whether it varies or remains constant, will tell us at once whether there has or has not been a tendency to alteration in the general form, or, in other words, a difference in the rates of growth in different directions. To this subject we shall return, when we come to consider more particularly the phenomenon of *rate of growth*.

double-hogshead. But Gilbert White of Selborne could not see what was plain to the Lilliputians; for finding that a certain little long-legged bird, the stilt, weighed $4\frac{1}{2}$ oz. and had legs 8 in. long, he thought that a flamingo, weighing 4 lbs., should have legs 10 ft. long, to be in the same proportion as the stilt's. But it is obvious to us that, as the weights of the two birds are as 1 : 15, so the legs (or other linear dimensions) should be as the cube-roots of these numbers, or nearly as 1 : $2\frac{1}{2}$. And on this scale the flamingo's legs should be, as they actually are, about 20 in. long.

We are accustomed to think of magnitude as a purely relative matter. We call a thing *big* or *little* with reference to what it is wont to be, as when we speak of a small elephant or a large rat; and we are apt accordingly to suppose that size makes no other or more essential difference, and that Lilliput and Brobdingnag* are all alike, according as we look at them through one end of the glass or the other. Gulliver himself declared, in Brobdingnag, that “undoubtedly philosophers are in the right when they tell us that nothing is great and little otherwise than by comparison”: and Oliver Heaviside used to say, in like manner, that there is no absolute scale of size in the Universe, for it is boundless towards the great and also boundless towards the small. It is of the very essence of the Newtonian philosophy that we should be able to extend our concepts and deductions from the one extreme of magnitude to the other; and Sir John Herschel said that “the student must lay his account to finding the distinction of great and little altogether annihilated in nature.”

All this is true of *number*, and of *relative magnitude*. The Universe has its endless gamut of great and small, of near and far, of many and few. Nevertheless, in physical science the scale of absolute magnitude becomes a very real and important thing; and a new and deeper interest arises out of the changing ratio of dimensions when we come to consider the inevitable changes of physical relations with which it is bound up. The effect of *scale* depends not on a thing in itself, but in relation to its whole environment or milieu; it is in conformity with the thing’s “place in Nature,” its field of action and reaction in the Universe. Everywhere Nature works true to scale, and everything has its proper size accordingly. Men and trees, birds and fishes, stars and star-systems, have their appropriate dimensions, and their more or less narrow range of absolute magnitudes. The scale of human observation and experience lies within the narrow bounds of inches, feet or miles, all measured in terms drawn from our own selves or our own doings. Scales which include light-years, parsecs, Ångström units, or atomic

* Swift paid close attention to the arithmetic of magnitude, but none to its physical aspect. See De Morgan, on Lilliput, in *N. and Q.* (2^y), vi, pp. 123–125, 1858. On relative magnitude see also Berkeley, in his *Essay towards a New Theory of Vision*, 1709.

and sub-atomic magnitudes, belong to other orders of things and other principles of cognition.

A common effect of scale is due to the fact that, of the physical forces, some act either directly at the surface of a body, or otherwise in proportion to its surface or area; while others, and above all gravity, act on all particles, internal and external alike, and exert a force which is proportional to the mass, and so, usually to the volume of the body.

A simple case is that of two similar weights hung by two similar wires. The forces exerted by the weights are proportional to their masses, and these to their volumes, and so to the cubes of the several linear dimensions, including the diameters of the wires. But the areas of cross-section of the wires are as the squares of the said linear dimensions; therefore the stresses in the wires *per unit area* are not identical, but increase in the ratio of the linear dimensions, and the larger the structure the more severe the strain becomes:

$$\frac{\text{Force}}{\text{Area}} \propto \frac{l^3}{l^2} \propto l,$$

and the less the wires are capable of supporting it.

In short, it often happens that of the forces in action in a system some vary as one power and some as another, of the masses, distances or other magnitudes involved; the "dimensions" remain the same in our equations of equilibrium, but the relative values alter with the scale. This is known as the "Principle of Similitude," or of dynamical similarity, and it and its consequences are of great importance. In a handful of matter cohesion, capillarity, chemical affinity, electric charge are all potent; across the solar system gravitation* rules supreme; in the mysterious region of the nebulae, it may haply be that gravitation grows negligible again.

To come back to homelier things, the strength of an iron girder obviously varies with the cross-section of its members, and each cross-section varies as the square of a linear dimension; but the weight of the whole structure varies as the cube of its linear dimen-

* In the early days of the theory of gravitation, it was deemed especially remarkable that the action of gravity "is proportional to the quantity of solid matter in bodies, and not to their surfaces as is usual in mechanical causes; this power, therefore, seems to surpass mere mechanism" (Colin Maclaurin, on *Sir Isaac Newton's Philosophical Discoveries*, iv, 9).

sions. It follows at once that, if we build two bridges geometrically similar, the larger is the weaker of the two*, and is so in the ratio of their linear dimensions. It was elementary engineering experience such as this that led Herbert Spencer to apply the principle of similitude to biology†.

But here, before we go further, let us take careful note that increased weakness is no necessary concomitant of increasing size. There are exceptions to the rule, in those exceptional cases where we have to deal only with forces which vary merely with the *area* on which they impinge. If in a big and a little ship two similar masts carry two similar sails, the two sails will be similarly strained, and equally stressed at homologous places, and alike suitable for resisting the force of the same wind. Two similar umbrellas, however differing in size, will serve alike in the same weather; and the expanse (though not the leverage) of a bird's wing may be enlarged with little alteration.

The principle of similitude had been admirably applied in a few clear instances by Lesage‡, a celebrated eighteenth-century physician, in an unfinished and unpublished work. Lesage argued, for example, that the larger ratio of surface to mass in a small animal would lead to excessive transpiration, were the skin as "porous" as our own; and that we may thus account for the hardened or thickened skins of insects and many other small terrestrial animals. Again, since the weight of a fruit increases as the cube of its linear dimensions, while the strength of the stalk increases as the square, it follows that the stalk must needs grow out of apparent due proportion to the fruit: or, alternatively, that tall trees should not bear large

* The subject is treated from the engineer's point of view by Prof. James Thomson, Comparison of similar structures as to elasticity, strength and stability, *Coll. Papers*, 1912, pp. 361-372, and *Trans. Inst. Engineers, Scotland*, 1876; also by Prof. A. Barr, *ibid.* 1899. See also Rayleigh, *Nature*, April 22, 1915; Sir G. Greenhill, On mechanical similitude, *Math. Gaz.* March 1916, *Coll. Works*, vi, p. 300. For a mathematical account, see (e.g.) P. W. Bridgeman, *Dimensional Analysis* (2nd ed.), 1931, or F. W. Lanchester, *The Theory of Dimensions*, 1936.

† Herbert Spencer, The form of the earth, etc., *Phil. Mag.* xxx, pp. 194-6, 1847; also *Principles of Biology*, pt. II, p. 123 seq., 1864.

‡ See Pierre Prévost, *Notices de la vie et des écrits de Lesage*, 1805. George Louis Lesage, born at Geneva in 1724, devoted sixty-three years of a life of eighty to a mechanical theory of gravitation; see W. Thomson (Lord Kelvin), On the ultramundane corpuscles of Lesage, *Proc. R.S.E.* vii, pp. 577-589, 1872; *Phil. Mag.* xlvi, pp. 321-345, 1873; and Clerk Maxwell, art. "Atom," *Encycl. Brit.* (9), p. 46.

fruit on slender branches, and that melons and pumpkins must lie upon the ground. And yet again, that in quadrupeds a large head must be supported on a neck which is either excessively thick and strong like a bull's, or very short like an elephant's*.

But it was Galileo who, wellnigh three hundred years ago, had first laid down this general principle of similitude; and he did so with the utmost possible clearness, and with a great wealth of illustration drawn from structures living and dead†. He said that if we tried building ships, palaces or temples of enormous size, yards, beams and bolts would cease to hold together; nor can Nature grow a tree nor construct an animal beyond a certain size, while retaining the proportions and employing the materials which suffice in the case of a smaller structure‡. The thing will fall to pieces of its own weight unless we either change its relative proportions, which will at length cause it to become clumsy, monstrous and inefficient, or else we must find new material, harder and stronger than was used before. Both processes are familiar to us in Nature and in art, and practical applications, undreamed of by Galileo, meet us at every turn in this modern age of cement and steel§.

Again, as Galileo was also careful to explain, besides the questions of pure stress and strain, of the strength of muscles to lift an increasing weight or of bones to resist its crushing stress, we have the important question of *bending moments*. This enters, more or less, into our whole range of problems; it affects the whole form of the skeleton, and sets a limit to the height of a tall tree||.

* Cf. W. Walton, On the debility of large animals and trees, *Quart. Journ. of Math.* ix, pp. 179–184, 1868; also L. J. Henderson, On volume in Biology, *Proc. Amer. Acad. Sci.* II, pp. 654–658, 1916; etc.

† *Discorsi e Dimostrazioni matematiche, intorno à due nuove scienze attenenti alla Mecanica ed ai Muovimenti Locali:* appresso gli Elzevirii, 1638; *Opere*, ed. Favaro, VIII, p. 169 seq. Transl. by Henry Crew and A. de Salvio, 1914, p. 130.

‡ So Werner remarked that Michael Angelo and Bramanti could not have built of gypsum at Paris on the scale they built of travertin at Rome.

§ The Chrysler and Empire State Buildings, the latter 1048 ft. high to the foot of its 200 ft. “mooring mast,” are the last word, at present, in this brobdingnagian architecture.

|| It was Euler and Lagrange who first shewed (about 1776–1778) that a column of a certain height would merely be compressed, but one of a greater height would be bent by its own weight. See Euler, *De altitudine columnarum etc.*, *Acta Acad. Sci. Imp. Petropol.* 1778, pp. 163–193; G. Greenhill, Determination of the greatest height to which a tree of given proportions can grow, *Cambr. Phil. Soc. Proc.* IV, p. 65, 1881, and Chree, *ibid.* VII, 1892.

We learn in elementary mechanics the simple case of two similar beams, supported at both ends and carrying no other weight than their own. Within the limits of their elasticity they tend to be deflected, or to sag downwards, in proportion to the squares of their linear dimensions; if a match-stick be two inches long and a similar beam six feet (or 36 times as long), the latter will sag under its own weight thirteen hundred times as much as the other. To counteract this tendency, as the size of an animal increases, the limbs tend to become thicker and shorter and the whole skeleton bulkier and heavier; bones make up some 8 per cent. of the body of mouse or wren, 13 or 14 per cent. of goose or dog, and 17 or 18 per cent. of the body of a man. Elephant and hippopotamus have grown clumsy as well as big, and the elk is of necessity less graceful than the gazelle. It is of high interest, on the other hand, to observe how little the skeletal proportions differ in a little porpoise and a great whale, even in the limbs and limb-bones; for the whole influence of gravity has become negligible, or nearly so, in both of these.

In the problem of the tall tree we have to determine the point at which the tree will begin to bend under its own weight if it be ever so little displaced from the perpendicular*. In such an investigation we have to make certain assumptions—for instance that the trunk tapers uniformly, and that the sectional area of the branches varies according to some definite law, or (as Ruskin assumed) tends to be constant in any horizontal plane; and the mathematical treatment is apt to be somewhat difficult. But Greenhill shewed, on such assumptions as the above, that a certain British Columbian pine-tree, of which the Kew flag-staff, which is 221 ft. high and 21 inches in diameter at the base, was made, could not possibly, by theory, have grown to more than about 300 ft. It is very curious that Galileo had suggested precisely the same height (*ducento braccie alta*) as the utmost limit of the altitude of a tree. In general, as Greenhill shewed, the diameter of a tall homogeneous body must increase as the power $3/2$ of its height, which accounts for the slender proportions of young trees compared with the squat

* In like manner the wheat-straw bends over under the weight of the loaded ear, and the cat's tail bends over when held erect—not because they "possess flexibility," but because they outstrip the dimensions within which stable equilibrium is possible in a vertical position. The kitten's tail, on the other hand, stands up spiky and straight.

or stunted appearance of old and large ones*. In short, as Goethe says in *Dichtung und Wahrheit*, "Es ist dafür gesorgt dass die Bäume nicht in den Himmel wachsen."

But the tapering pine-tree is but a special case of a wider problem. The oak does not grow so tall as the pine-tree, but it carries a heavier load, and its boll, broad-based upon its spreading roots, shews a different contour. Smeaton took it for the pattern of his lighthouse, and Eiffel built his great tree of steel, a thousand feet high, to a similar but a stricter plan. Here the profile of tower or tree follows, or tends to follow, a logarithmic curve, giving equal strength throughout, according to a principle which we shall have occasion to discuss later on, when we come to treat of form and mechanical efficiency in the skeletons of animals. In the tree, moreover, anchoring roots form powerful wind-struts, and are most developed opposite to the direction of the prevailing winds; for the lifetime of a tree is affected by the frequency of storms, and its strength is related to the wind-pressure which it must needs withstand†.

Among animals we see, without the help of mathematics or of physics, how small birds and beasts are quick and agile, how slower and sedater movements come with larger size, and how exaggerated bulk brings with it a certain clumsiness, a certain inefficiency, an element of risk and hazard, a preponderance of disadvantage. The case was well put by Owen, in a passage which has an interest of its own as a premonition, somewhat like De Candolle's, of the "struggle for existence." Owen wrote as follows‡: "In proportion to the bulk of a species is the difficulty of the contest which, as a living organised whole, the individual of each species has to maintain against the surrounding agencies that are ever tending to dissolve the vital bond, and subjugate the living matter to the ordinary chemical and physical forces. Any changes, therefore, in such external conditions as a species may have been originally adapted

* The stem of the giant bamboo may attain a height of 60 metres while not more than about 40 cm. in diameter near its base, which dimensions fall not far short of the theoretical limits; A. J. Ewart, *Phil. Trans.* cxcviii, p. 71, 1906.

† Cf. (*int. al.*) T. Petch, On buttress tree-roots, *Ann. R. Bot. Garden, Peradeniya*, xi, pp. 277-285, 1930. Also an interesting paper by James Macdonald, on The form of coniferous trees, *Forestry*, vi, 1 and 2, 1931/2.

‡ *Trans. Zool. Soc.* iv, p. 27, 1850.

to exist in, will militate against that existence in a degree proportionate, perhaps in a geometrical ratio, to the bulk of the species. If a dry season be greatly prolonged, the large mammal will suffer from the drought sooner than the small one; if any alteration of climate affect the quantity of vegetable food, the bulky Herbivore will be the first to feel the effects of stinted nourishment."

But the principle of Galileo carries us further and along more certain lines. The strength of a muscle, like that of a rope or girder, varies with its cross-section; and the resistance of a bone to a crushing stress varies, again like our girder, with its cross-section. But in a terrestrial animal the weight which tends to crush its limbs, or which its muscles have to move, varies as the cube of its linear dimensions; and so, to the possible magnitude of an animal, living under the direct action of gravity, there is a definite limit set. The elephant, in the dimensions of its limb-bones, is already shewing signs of a tendency to disproportionate thickness as compared with the smaller mammals; its movements are in many ways hampered and its agility diminished: it is already tending towards the maximal limit of size which the physical forces permit*. The spindleshanks of gnat or daddy-long-legs have their own factor of safety, conditional on the creature's exiguous bulk and weight; for after their own fashion even these small creatures tend towards an inevitable limitation of their natural size. But, as Galileo also saw, if the animal be wholly immersed in water like the whale, or if it be partly so, as was probably the case with the giant reptiles of the mesozoic age, then the weight is counterpoised to the extent of an equivalent volume of water, and is completely counterpoised if the density of the animal's body, with the included air, be identical (as a whale's very nearly is) with that of the water around†. Under these circumstances there is no longer the same physical barrier to the indefinite growth of the animal. Indeed, in the case of the aquatic animal, there is, as Herbert Spencer pointed out,

* Cf. A. Rauber, Galileo über Knochenformen, *Morphol. Jahrb.* VII, p. 327, 1882.

† Cf. W. S. Wall, *A New Sperm Whale etc.*, Sydney, 1851, p. 64: "As for the immense size of Cetacea, it evidently proceeds from their buoyancy in the medium in which they live, and their being enabled thus to counteract the force of gravity."

a distinct advantage, in that the larger it grows the greater is its speed. For its available energy depends on the mass of its muscles, while its motion through the water is opposed, not by gravity, but by "skin-friction," which increases only as the square of the linear dimensions*: whence, other things being equal, the bigger the ship or the bigger the fish the faster it tends to go, but only in the ratio of the square root of the increasing length. For the velocity (V) which the fish attains depends on the work (W) it can do and the resistance (R) it must overcome. Now we have seen that the dimensions of W are l^3 , and of R are l^2 ; and by elementary mechanics

$$W \propto RV^2, \text{ or } V^2 \propto \frac{W}{R}.$$

Therefore $V^2 \propto \frac{l^3}{l^2} = l$, and $V \propto \sqrt{l}$.

This is what is known as *Froude's Law*, of the correspondence of speeds—a simple and most elegant instance of "dimensional theory†."

But there is often another side to these questions, which makes them too complicated to answer in a word. For instance, the work (per stroke) of which two similar engines are capable should vary as the cubes of their linear dimensions, for it varies on the one hand with the *area* of the piston, and on the other with the *length* of the stroke; so is it likewise in the animal, where the corresponding ratio depends on the cross-section of the muscle, and on the distance through which it contracts. But in two similar engines, the available horse-power varies as the square of the linear dimensions, and not as the cube; and this for the reason that the actual *energy* developed depends on the heating-surface of the boiler‡. So likewise must

* We are neglecting "drag" or "head-resistance," which, increasing as the cube of the speed, is a formidable obstacle to an unstreamlined body. But the perfect streamlining of whale or fish or bird lets the surrounding air or water behave like a perfect fluid, gives rise to no "surface of discontinuity," and the creature passes through it without recoil or turbulence. Froude reckoned skin-friction, or surface-resistance, as equal to that of a *plane* as long as the vessel's water-line, and of area equal to that of the wetted surface of the vessel.

† Though, as Lanchester says, the great designer "was not hampered by a knowledge of the theory of dimensions."

‡ The analogy is not a very strict or complete one. We are not taking account, for instance, of the thickness of the boiler-plates.

there be a similar tendency among animals for the rate of supply of kinetic energy to vary with the surface of the lung, that is to say (other things being equal) with the *square* of the linear dimensions of the animal; which means that, *caeteris paribus*, the small animal is stronger (having more power per unit weight) than a large one. We may of course (departing from the condition of similarity) increase the heating-surface of the boiler, by means of an internal system of tubes, without increasing its outward dimensions, and in this very way Nature increases the respiratory surface of a lung by a complex system of branching tubes and minute air-cells; but nevertheless in two similar and closely related animals, as also in two steam-engines of the same make, the law is bound to hold that the rate of working tends to vary with the square of the linear dimensions, according to Froude's *law of steamship comparison*. In the case of a very large ship, built for speed, the difficulty is got over by increasing the size and number of the boilers, till the ratio between boiler-room and engine-room is far beyond what is required in an ordinary small vessel*; but though we find lung-space increased among animals where greater rate of working is required, as in general among birds, I do not know that it can be shewn to increase, as in the "over-boilered" ship, with the size of the animal, and in a ratio which outstrips that of the other bodily dimensions. If it be the case then, that the working mechanism of the muscles should be able to exert a force proportionate to the cube of the linear bodily dimensions,

* Let L be the length, S the (wetted) surface, T the tonnage, D the displacement (or volume) of a ship; and let it cross the Atlantic at a speed V . Then, in comparing two ships, similarly constructed but of different magnitudes, we know that $L = V^2$, $S = L^2 = V^4$, $D = T = L^3 = V^6$; also R (resistance) $= S \cdot V^2 = V^8$; H (horse-power) $= R \cdot V = V^7$; and the coal (C) necessary for the voyage $= H/V = V^6$. That is to say, in ordinary engineering language, to increase the speed across the Atlantic by 1 per cent. the ship's length must be increased 2 per cent., her tonnage or displacement 6 per cent., her coal-consumption also 6 per cent., her horse-power, and therefore her boiler-capacity, 7 per cent. Her bunkers, accordingly, keep pace with the enlargement of the ship, but her boilers tend to increase out of proportion to the space available. Suppose a steamer 400 ft. long, of 2000 tons, 2000 h.p., and a speed of 14 knots. The corresponding vessel of 800 ft. long should develop a speed of 20 knots ($1 : 2 :: 14^2 : 20^2$), her tonnage would be 16,000, her h.p. 25,000 or thereby. Such a vessel would probably be driven by four propellers instead of one, each carrying 8000 h.p. See (*int. al.*) W. J. Millar, On the most economical speed to drive a steamer, *Proc. Edin. Math. Soc.* vii, pp. 27-29, 1889; Sir James R. Napier, On the most profitable speed for a fully laden cargo steamer for a given voyage, *Proc. Phil. Soc., Glasgow*, vi, pp. 33-38, 1865.

while the respiratory mechanism can only supply a store of energy at a rate proportional to the square of the said dimensions, the singular result ought to follow that, in swimming for instance, the larger fish ought to be able to put on a spurt of speed far in excess of the smaller one; but the distance travelled by the year's end should be very much alike for both of them. And it should also follow that the curve of fatigue is a steeper one, and the staying power less, in the smaller than in the larger individual. This is the case in long-distance racing, where neither draws far ahead until the big winner puts on his big spurt at the end; on which is based an aphorism of the turf, that "a good big 'un is better than a good little 'un." For an analogous reason wise men know that in the 'Varsity boat-race it is prudent and judicious to bet on the heavier crew.

Consider again the dynamical problem of the movements of the body and the limbs. The work done (W) in moving a limb, whose weight is p , over a distance s , is measured by ps ; p varies as the cube of the linear dimensions, and s , in ordinary locomotion, varies as the linear dimensions, that is to say as the length of limb:

$$W \propto ps \propto l^3 \times l = l^4.$$

But the work done is limited by the power available, and this varies as the mass of the muscles, or as l^3 ; and under this limitation neither p nor s increase as they would otherwise tend to do. The limbs grow shorter, relatively, as the animal grows bigger; and spiders, daddy-long-legs and such-like long-limbed creatures attain no great size.

Let us consider more closely the actual energies of the body. A hundred years ago, in Strasburg, a physiologist and a mathematician were studying the temperature of warm-blooded animals*. The heat lost must, they said, be proportional to the surface of the animal: and the gain must be equal to the loss, since the temperature of the body keeps constant. It would seem, therefore, that the heat lost by radiation and that gained by oxidation vary both alike, as the surface-area, or the square of the linear dimensions, of the animal. But this result is paradoxical; for whereas the heat lost

* MM. Rameaux et Sarrus, *Bull. Acad. R. de Médecine*, III, pp. 1094–1100, 1838–39.

may well vary as the surface-area, that produced by oxidation ought rather to vary as the bulk of the animal: one should vary as the square and the other as the cube of the linear dimensions. Therefore the ratio of loss to gain, like that of surface to volume, ought to increase as the size of the creature diminishes. Another physiologist, Carl Bergmann*, took the case a step further. It was he, by the way, who first said that the real distinction was not between warm-blooded and cold-blooded animals, but between those of constant and those of variable temperature: and who coined the terms *homœothermic* and *poecilothermic* which we use today. He was driven to the conclusion that the smaller animal does produce more heat (per unit of mass) than the large one, in order to keep pace with surface-loss; and that this extra heat-production means more energy spent, more food consumed, more work done†. Simplified as it thus was, the problem still perplexed the physiologists for years after. The tissues of one mammal are much like those of another. We can hardly imagine the muscles of a small mammal to produce more heat (*caeteris paribus*) than those of a large; and we begin to wonder whether it be not nervous excitation, rather than quality of muscular tissue, which determines the rate of oxidation and the output of heat. It is evident in certain cases, and may be a general rule, that the smaller animals have the bigger brains; "plus l'animal est petit," says M. Charles Richet, "plus il a des échanges chimiques actifs, et plus son cerveau est volumineux‡." That the smaller animal needs more food is certain and obvious. The amount of food and oxygen consumed by a small flying insect is enormous; and bees and flies and hawkmoths and humming-

* Carl Bergmann, *Verhältnisse der Wärmeökonomie der Tiere zu ihrer Grösse*, *Göttinger Studien*, I, pp. 594–708, 1847—a very original paper.

† The metabolic activity of sundry mammals, per 24 hours, has been estimated as follows:

	Weight (kilo.)	Calories per kilo.
Guinea-pig	0·7	223
Rabbit	2	58
Man	70	33
Horse	600	22
Elephant	4000	13
Whale	150000	<i>circa</i> 1·7

‡ Ch. Richet, *Recherches de calorimétrie*, *Arch. de Physiologie* (3), VI, pp. 237–291, 450–497, 1885. Cf. also an interesting historical account by M. Elie le Breton, *Sur la notion de "masse protoplasmique active"*: i. *Problèmes posés par la signification de la loi des surfaces*, *ibid.* 1906, p. 606.

birds live on nectar, the richest and most concentrated of foods*. Man consumes a fiftieth part of his own weight of food daily, but a mouse will eat half its own weight in a day; its rate of living is faster, it breeds faster, and old age comes to it much sooner than to man. A warm-blooded animal much smaller than a mouse becomes an impossibility; it could neither obtain nor yet digest the food required to maintain its constant temperature, and hence no mammals and no birds are as small as the smallest frogs or fishes. The disadvantage of small size is all the greater when loss of heat is accelerated by conduction as in the Arctic, or by convection as in the sea. The far north is a home of large birds but not of small; bears but not mice live through an Arctic winter; the least of the dolphins live in warm waters, and there are no small mammals in the sea. This principle is sometimes spoken of as *Bergmann's Law*.

The whole subject of the conservation of heat and the maintenance of an all but constant temperature in warm-blooded animals interests the physicist and the physiologist alike. It drew Kelvin's attention many years ago†, and led him to shew, in a curious paper, how larger bodies are kept warm by clothing while smaller are only cooled the more. If a current be passed through a thin wire, of which part is covered and part is bare, the thin bare part may glow with heat, while convection-currents streaming round the covered part cool it off and leave it in darkness. The hairy coat of very small animals is apt to look thin and meagre, but it may serve them better than a shaggier covering.

Leaving aside the question of the supply of energy, and keeping to that of the mechanical efficiency of the machine, we may find endless biological illustrations of the principle of similitude. All through the physiology of locomotion we meet with it in various ways: as, for instance, when we see a cockchafer carry a plate many times its own weight upon its back, or a flea jump many inches high. "A dog," says Galileo, "could probably carry two or three such dogs upon his back; but I believe that a horse could not carry even one of his own size."

* Cf. R. A. Davies and G. Fraenkel, The oxygen-consumption of flies during flight, *Jl. Exp. Biol.* xvii, pp. 402-407, 1940.

† W. Thomson, On the efficiency of clothing for maintaining temperature, *Nature*, xxix, p. 567, 1884.

Such problems were admirably treated by Galileo and Borelli, but many writers remained ignorant of their work. Linnaeus remarked that if an elephant were as strong in proportion as a stag-beetle, it would be able to pull up rocks and level mountains; and Kirby and Spence have a well-known passage directed to shew that such powers as have been conferred upon the insect have been withheld from the higher animals, for the reason that had these latter been endued therewith they would have "caused the early desolation of the world*."

Such problems as that presented by the flea's jumping powers†, though essentially physiological in their nature, have their interest for us here: because a steady, progressive diminution of activity with increasing size would tend to set limits to the possible growth in magnitude of an animal just as surely as those factors which tend to break and crush the living fabric under its own weight. In the case of a leap, we have to do rather with a sudden impulse than with a continued strain, and this impulse should be measured in terms of the velocity imparted. The velocity is proportional to the impulse (x), and inversely proportional to the mass (M) moved: $V = x/M$. But, according to what we still speak of as "Borelli's law," the impulse (i.e. the work of the impulse) is proportional to the volume of the muscle by which it is produced‡, that is to say (in similarly constructed animals) to the mass of the whole body; for the impulse is proportional on the one hand to the cross-section of the muscle, and on the other to the distance through which it

* *Introduction to Entomology*, II, p. 190, 1826. Kirby and Spence, like many less learned authors, are fond of popular illustrations of the "wonders of Nature," to the neglect of dynamical principles. They suggest that if a white ant were as big as a man, its tunnels would be "magnificent cylinders of more than three hundred feet in diameter"; and that if a certain noisy Brazilian insect were as big as a man, its voice would be heard all the world over, "so that Stentor becomes a mute when compared with these insects!" It is an easy consequence of anthropomorphism, and hence a common characteristic of fairy-tales, to neglect the dynamical and dwell on the geometrical aspect of similarity.

† The flea is a very clever jumper; he jumps backwards, is stream-lined accordingly, and alights on his two long hind-legs. Cf. G. I. Watson, in *Nature*, 21 May 1938.

‡ That is to say, the available energy of muscle, in ft.-lbs. per lb. of muscle, is the same for all animals: a postulate which requires considerable qualification when we come to compare very different kinds of muscle, such as the insect's and the mammal's.

contracts. It follows from this that the velocity is constant, whatever be the size of the animal.

Putting it still more simply, the work done in leaping is proportional to the mass and to the height to which it is raised, $W \propto mH$. But the muscular power available for this work is proportional to the mass of muscle, or (in similarly constructed animals) to the mass of the animal, $W \propto m$. It follows that H is, or tends to be, a constant. In other words, all animals, provided always that they are similarly fashioned, with their various levers in like proportion, ought to jump not to the same relative but to the same *actual* height*. The grasshopper seems to be as well planned for jumping as the flea, and the actual heights to which they jump are much of a muchness; but the flea's jump is about 200 times its own height, the grasshopper's at most 20-30 times; and neither flea nor grasshopper is a better but rather a worse jumper than a horse or a man†.

As a matter of fact, Borelli is careful to point out that in the act of leaping the impulse is not actually instantaneous, like the blow of a hammer, but takes some little time, during which the levers are being extended by which the animal is being propelled forwards; and this interval of time will be longer in the case of the longer levers of the larger animal. To some extent, then, this principle acts as a corrective to the more general one, and tends to leave a certain balance of advantage in regard to leaping power on the side of the larger animal‡. But on the other hand, the question of strength of materials comes in once more, and the factors of stress and strain and bending moment make it more and more difficult for nature to endow the larger animal with the length of lever with which she has provided the grasshopper or the flea. To Kirby and Spence it seemed that "This wonderful strength of insects is doubtless the result of something peculiar in the structure and arrangement of their muscles, and principally their extraordinary

* Borelli, Prop. CLXXVII. *Animalia minora et minus ponderosa maiores saltus efficiunt respectu sui corporis, si caetera fuerint paria.*

† The high jump is nowadays a highly skilled performance. For the jumper contrives that his centre of gravity goes *under* the bar, while his body, bit by bit, goes *over* it.

‡ See also (*int. al.*), John Bernoulli, *De Motu Muscularum*, Basil., 1694; Chabry, *Mécanisme du saut*, *J. de l'Anat. et de la Physiol.* XIX, 1883; *Sur la longueur des membres des animaux sauteurs*, *ibid.* XXI, p. 356, 1885; Le Hello, *De l'action des organes locomoteurs*, etc., *ibid.* XXIX, pp. 65-93, 1893; etc.

power of contraction." This hypothesis, which is so easily seen on physical grounds to be unnecessary, has been amply disproved in a series of excellent papers by Felix Plateau*.

From the *impulse* of the preceding case we may pass to the *momentum* created (or destroyed) under similar circumstances by a given force acting for a given time: $mv=Ft$.

We know that $m \propto l^3$, and $t=l/v$,
so that $l^3v=Fl/v$, or $v^2=F/l^2$.

But whatsoever force be available, the animal may only exert so much of it as is in proportion to the strength of his own limbs, that is to say to the cross-section of bone, sinew and muscle; and all of these cross-sections are proportional to l^2 , the square of the linear dimensions. The maximal force, F_{\max} , which the animal *dare* exert is proportional, then, to l^2 ; therefore

$$F_{\max}/l^2 = \text{constant}.$$

And the maximal speed which the animal can safely reach, namely $V_{\max}=F_{\max}/l$, is also constant, or independent (*ceteris paribus*) of the dimensions of the animal.

A spurt or effort may be well within the capacity of the animal but far beyond the margin of safety, as trainer and athlete well know. This margin is a narrow one, whether for athlete or racehorse; both run a constant risk of overstrain, under which they may "pull" a muscle, lacerate a tendon, or even "break down" a bone†.

It is fortunate for their safety that animals do not jump to heights proportional to their own. For conceive an animal (of mass m) to jump to a certain altitude, such that it reaches the ground with a velocity v ; then if c be the crushing strain at any point of the sectional area (A) of the limbs, the limiting condition is that $mv=cA$.

If the animal vary in magnitude without change in the height to which it jumps (or in the velocity with which it descends), then

$$c \propto \frac{m}{A} \propto \frac{l^3}{l^2}, \text{ or } l.$$

The crushing strain varies directly with the linear dimensions of the animal; and this, a dynamical case, is identical with the usual statical limitation of magnitude.

* Recherches sur la force absolue des muscles des Invertébrés, *Bull. Acad. R. de Belgique* (3), vi, vii, 1883–84: see also *ibid.* (2), xx, 1865; xxii, 1866; *Ann. Mag. N.H.* xvii, p. 139, 1866; xix, p. 95, 1867. Cf. M. Radau, Sur la force musculaire des insectes, *Revue des deux Mondes*, lxiv, p. 770, 1866. The subject had been well treated by Straus-Dürckheim, in his *Considérations générales sur l'anatomie comparée des animaux articulés*, 1828.

† Cf. The dynamics of sprint-running, by A. V. Hill and others, *Proc. R.S. (B)*, cii, pp. 29–42, 1927; or *Muscular Movement in Man*, by A. V. Hill, New York, 1927, ch. vi, p. 41.

But if the animal, with increasing size or stature, jump to a correspondingly increasing height, the case becomes much more serious. For the final velocity of descent varies as the square root of the altitude reached, and therefore as the square root of the linear dimensions of the animal. And since, as before,

$$c \propto mv \propto \frac{l^3}{l^2} V,$$

$$\therefore c \propto \frac{l^2}{l^2} \sqrt{V}, \text{ or } c \propto l^{\frac{1}{2}}.$$

If a creature's jump were in proportion to its height, the crushing strains would so increase that its dimensions would be limited thereby in a much higher degree than was indicated by statical considerations. An animal may grow to a size where it is unstable dynamically, though still on the safe side statically—a size where it moves with difficulty though it rests secure. It is by reason of dynamical rather than of statical relations that an elephant is of graver deportment than a mouse.

An apparently simple problem, much less simple than it looks, lies in the act of walking, where there will evidently be great economy of work if the leg swing with the help of gravity, that is to say, at a *pendulum-rate*. The conical shape and jointing of the limb, the time spent with the foot upon the ground, these and other mechanical differences complicate the case, and make the rate hard to define or calculate. Nevertheless, we may convince ourselves by counting our steps, that the leg does actually tend to swing, as a pendulum does, at a certain definite rate*. So on the same principle, but to the slower beat of a longer pendulum, the scythe swings smoothly in the mower's hands.

To walk quicker, we "step out"; we cause the leg-pendulum to describe a greater arc, but it does not swing or vibrate faster until we shorten the pendulum and begin to run. Now let two similar individuals, *A* and *B*, walk in a similar fashion, that is to say with a similar *angle* of swing (Fig. 1). The *arc* through which the leg swings, or the *amplitude* of each step, will then vary as the length of leg (say as *a/b*), and so as the height or other linear dimension (*l*) of the man†. But the time of swing varies inversely as the square

* The assertion that the limb tends to swing in pendulum-time was first made by the brothers Weber (*Mechanik der menschl. Gehwerkzeuge*, Göttingen, 1836). Some later writers have criticised the statement (e.g. Fischer, *Die Kinematik des Beinschwingens etc.*, *Abh. math. phys. Kl. k. Sächs. Ges.* xxv–xxviii, 1899–1903), but for all that, with proper and large qualifications, it remains substantially true.

† So the stride of a Brobdingnagian was 10 yards long, or just twelve times the 2 ft. 6 in., which make the average stride or half-pace of a man.

root of the pendulum-length, or \sqrt{a}/\sqrt{b} . Therefore the velocity, which is measured by amplitude/time, or $a/b \times \sqrt{b}/\sqrt{a}$, will also vary as the square root of the linear dimensions; which is Froude's law over again.

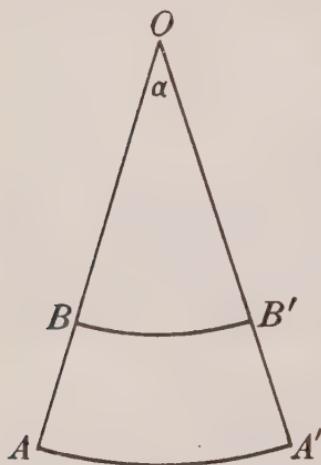


Fig. 1.

The smaller man, or smaller animal, goes slower than the larger, but only in the ratio of the square roots of their linear dimensions; whereas, if the limbs moved alike, irrespective of the size of the animal—if the limbs of the mouse swung no faster than those of the horse—then the mouse would be as slow in its gait or slower than the tortoise. M. Delisle* saw a fly walk three inches in half-a-second; this was good steady walking. When we walk five miles an hour we go about 88 inches in a second,

or $88/6 = 14.7$ times the pace of M. Delisle's fly. We should walk at just about the fly's pace if our stature were $1/(14.7)^2$, or $1/216$ of our present height—say 72/216 inches, or one-third of an inch high. Let us note in passing that the number of legs does not matter, any more than the number of wheels to a coach; the centipede runs none the faster for all his hundred legs.

But the leg comprises a complicated system of levers, by whose various exercise we obtain very different results. For instance, by being careful to rise upon our instep we increase the length or amplitude of our stride, and improve our speed very materially; and it is curious to see how Nature lengthens this metatarsal joint, or instep-lever, in horse† and hare and greyhound, in ostrich and in kangaroo, and in every speedy animal. Furthermore, in running we bend and so shorten the leg, in order to accommodate it to a quicker rate of pendulum-swing‡. In short the jointed structure

* Quoted in Mr John Bishop's interesting article in Todd's *Cyclopaedia*, III, p. 443.

† The "cannon-bones" are not only relatively longer but may even be actually longer in a little racehorse than a great carthorse.

‡ There is probably another factor involved here: for in bending and thus shortening the leg, we bring its centre of gravity nearer to the pivot, that is to

of the leg permits us to use it as the shortest possible lever while it is swinging, and as the longest possible lever when it is exerting its propulsive force.

The bird's case is of peculiar interest. In running, walking or swimming, we consider the speed which an animal *can attain*, and the increase of speed which increasing size permits of. But in flight there is a certain necessary speed—a speed (relative to the air) which the bird *must attain* in order to maintain itself aloft, and which *must* increase as its size increases. It is highly probable, as Lanchester remarks, that Lilienthal met his untimely death (in August 1896) not so much from any intrinsic fault in the design or construction of his machine, but simply because his speed fell somewhat short of that necessary for stability.

Twenty-five years ago, when this book was written, the bird, or the aeroplane, was thought of as a machine whose sloping wings, held at a given angle and driven horizontally forward, deflect the air downwards and derive support from the upward reaction. In other words, the bird was supposed to communicate to a mass of air a downward momentum equivalent (in unit time) to its own weight, and to do so by direct and continuous impact. The downward momentum is then proportional to the mass of air thrust downwards, and to the rate at which it is so thrust or driven; the mass being proportional to the wing-area and to the speed of the bird, and the rate being again proportional to the flying speed; so that the momentum varies as the square of the bird's linear dimensions and also as the square of its speed. But in order to balance its weight, this momentum must also be proportional to the cube of the bird's linear dimensions; therefore the bird's necessary speed, such as enables it to maintain level flight, must be proportional to the square root of its linear dimensions, and the whole work done must be proportional to the power $3\frac{1}{2}$ of the said linear dimensions.

The case stands, so far, as follows: m , the mass of air deflected downwards; M , the momentum so communicated; W , the work done—all in unit time; w , the weight, and V , the velocity of the say to the joint, and so the muscle tends to move it more quickly. After all we know that the pendulum theory is not the whole story, but only an important first approximation to a complex phenomenon.

bird; l , a linear dimension, the form of the bird being supposed constant. $M = w = l^3$, but $M = mV$, and $m = l^2V$.

$$\begin{aligned} \text{Therefore} \quad M &= l^2V^2 = l^3, \\ \text{and therefore} \quad V &= \sqrt{l} \\ \text{and} \quad W &= MV = l^{3\frac{1}{2}}. \end{aligned}$$

The gist of the matter is, or seems to be, that the work which *can be done* varies with the available weight of muscle, that is to say, with the mass of the bird; but the work which *has to be done* varies with mass and distance; so the larger the bird grows, the greater the disadvantage under which all its work is done*. The disproportion does not seem very great at first sight, but it is quite enough to tell. It is as much as to say that, every time we double the linear dimensions of the bird, the difficulty of flight, or the work which must needs be done in order to fly, is increased in the ratio of 2^3 to $2^{3\frac{1}{2}}$, or $1 : \sqrt{2}$, or say $1 : 1.4$. If we take the ostrich to exceed the sparrow in linear dimensions as $25 : 1$, which seems well within the mark, the ratio would be that between $25^{3\frac{1}{2}}$ and 25^3 , or between 5^7 and 5^6 ; in other words, flight would be five times more difficult for the larger than for the smaller bird.

But this whole explanation is doubly inadequate. For one thing, it takes no account of *gliding flight*, in which energy is drawn from the wind, and neither muscular power nor engine power are employed; and we see that the larger birds, vulture, albatross or solan-goose, depend on gliding more and more. Secondly, the old simple account of the impact of the wing upon the air, and the manner in which a downward momentum is communicated and support obtained, is now known to be both inadequate and erroneous. For the science of flight, or aerodynamics, has grown out of the older science of hydrodynamics; both deal with the special properties of a fluid, whether water or air; and in our case, to be content to think of the air as a body of mass m , to which a velocity v is imparted, is to neglect all its fluid properties. How the

* This is the result arrived at by Helmholtz, Ueber ein Theorem geometrisch-ähnliche Bewegungen flüssiger Körper betreffend, nebst Anwendung auf das Problem Luftballons zu lenken, *Monatsber. Akad. Berlin*, 1873, pp. 501–514. It was criticised and challenged (somewhat rashly) by K. Müllenhoef, Die Grösse der Flugflächen etc., *Pflüger's Archiv*, xxxv, p. 407; xxxvi, p. 548, 1885.

fish or the dolphin swims, and how the bird flies, are up to a certain point analogous problems; and *stream-lining* plays an essential part in both. But the bird is much heavier than the air, and the fish has much the same density as the water, so that the problem of keeping afloat or aloft is negligible in the one, and all-important in the other. Furthermore, the one fluid is highly compressible, and the other (to all intents and purposes) incompressible; and it is this very difference which the bird, or the aeroplane, takes special advantage of, and which helps, or even enables, it to fly.

It remains as true as ever that a bird, in order to counteract gravity, must cause air to move downward and obtains an upward reaction thereby. But the air displaced downward beneath the wing accounts for a small and varying part, perhaps a third perhaps a good deal less, of the whole force derived; and the rest is generated above the wing, in a less simple way. For, as the air streams past the slightly sloping wing, as smoothly as the stream-lined form and polished surface permit, it swirls round the front or "leading" edge*, and then streams swiftly over the upper surface of the wing; while it passes comparatively slowly, checked by the opposing slope of the wing, across the lower side. And this is as much as to say that it tends to be compressed below and rarefied above; in other words, that a partial vacuum is formed above the wing and follows it wherever it goes, so long as the stream-lining of the wing and its angle of incidence are suitable, and so long as the bird travels fast enough through the air.

The bird's weight is exerting a downward force upon the air, in one way just as in the other; and we can imagine a barometer delicate enough to shew and measure it as the bird flies overhead. But to calculate that force we should have to consider a multitude of component elements; we should have to deal with the stream-lined tubes of flow above and below, and the eddies round the fore-edge of the wing and elsewhere; and the calculation which was too simple before now becomes insuperably difficult. But the principle of necessary speed remains as true as ever. The bigger the bird

* The arched form, or "dipping front edge" of the wing, and its use in causing a vacuum above, were first recognised by Mr H. F. Phillips, who put the idea into a patent in 1884. The facts were discovered independently, and soon afterwards, both by Lilienthal and Lanchester.

becomes, the more swiftly must the air stream over the wing to give rise to the rarefaction or negative pressure which is more and more required; and the harder must it be to fly, so long as work has to be done by the muscles of the bird. The general principle is the same as before, though the quantitative relation does not work out as easily as it did. As a matter of fact, there is probably little difference in the end; and in aeronautics, the "total resultant force" which the bird employs for its support is said, *empirically*, to vary as the square of the air-speed: which is then a result analogous to Froude's law, and is just what we arrived at before in the simpler and less accurate setting of the case.

But a comparison between the larger and the smaller bird, like all other comparisons, applies only so long as the other factors in the case remain the same; and these vary so much in the complicated action of flight that it is hard indeed to compare one bird with another. For not only is the bird continually changing the incidence of its wing, but it alters the lie of every single important feather; and all the ways and means of flight vary so enormously, in big wings and small, and Nature exhibits so many refinements and "improvements" in the mechanism required, that a comparison based on size alone becomes imaginary, and is little worth the making.

The above considerations are of great practical importance in aeronautics, for they shew how a provision of increasing speed *must* accompany every enlargement of our aeroplanes. Speaking generally, the necessary or minimal speed of an aeroplane varies as the square root of its linear dimensions; if (*ceteris paribus*) we make it four times as long, it must, in order to remain aloft, fly twice as fast as before*. If a given machine weighing, say, 500 lb. be stable at 40 miles an hour, then a geometrically similar one which weighs, say, a couple of tons has its speed determined as follows:

$$W:w::L^3:l^3::8:1.$$

Therefore

$$L:l::2:1.$$

But

$$V^2:v^2::L:l.$$

Therefore

$$V:v::\sqrt{2}:1 = 1.414:1.$$

* G. H. Bryan, *Stability in Aviation*, 1911; F. W. Lanchester, *Aerodynamics*, 1909; cf. (*int. al.*) George Greenhill, *The Dynamics of Mechanical Flight*, 1912; F. W. Headley, *The Flight of Birds*, and recent works.

That is to say, the larger machine must be capable of a speed of 40×1.414 , or about $56\frac{1}{2}$, miles per hour.

An arrow is a somewhat rudimentary flying-machine; but it is capable, to a certain extent and at a high velocity, of acquiring "stability," and hence of actual flight after the fashion of an aeroplane; the duration and consequent range of its trajectory are vastly superior to those of a bullet of the same initial velocity. Coming back to our birds, and again comparing the ostrich with the sparrow, we find we know little or nothing about the actual speed of the latter; but the minimal speed of the swift is estimated at 100 ft. per second, or even more—say 70 miles an hour. We shall be on the safe side, and perhaps not far wrong, to take 20 miles an hour as the sparrow's minimal speed; and it would then follow that the ostrich, of 25 times the sparrow's linear dimensions, would have to fly (if it flew at all) with a minimum velocity of 5×20 , or 100 miles an hour*.

The same principle of *necessary speed*, or the inevitable relation between the dimensions of a flying object and the minimum velocity at which its flight is stable, accounts for a considerable number of

* Birds have an ordinary and a forced speed. Meinertzhangen puts the ordinary flight of the swift at 68 m.p.h., which tallies with the old estimate of Athanasius Kircher (*Physiologia*, ed. 1680, p. 65) of 100 ft. per second for the swallow. Abel Chapman (*Retrospect*, 1928, ch. xiv) puts the gliding or swooping flight of the swift at over 150 m.p.h., and that of the griffon vulture at 180 m.p.h.; but these skilled fliers doubtless far exceed the necessary minimal speeds which we are speaking of. An airman flying at 70 m.p.h. has seen a golden eagle fly past him easily; but even this speed is exceptional. Several observers agree in giving 50 m.p.h. for grouse and woodcock, and 30 m.p.h. for starling, chaffinch, quail and crow. A migrating flock of lapwing travelled at 41 m.p.h., ten or twelve miles more than the usual speed of the single bird. Lanchester, on theoretical considerations, estimates the speed of the herring gull at 26 m.p.h., and of the albatross at about 34 miles. A tern, a very skilful flier, was seen to fly as slowly as 15 m.p.h. A hornet or a large dragonfly may reach 14 or 18 m.p.h.; but for most insects 2–4 metres per sec., say 4–9 m.p.h., is a common speed (cf. A. Magnan, *Vol. des Insectes*, 1834, p. 72). The larger diptera are very swift, but their speed is much exaggerated. A deerfly (*Cephenomyia*) has been said to fly at 400 yards per second, or say 800 m.p.h., an impossible velocity (Irving Langmuir, *Science*, March 11, 1938). It would mean a pressure on the fly's head of half an atmosphere, probably enough to crush the fly; to maintain it would take half a horsepower; and this would need a food-consumption of $1\frac{1}{2}$ times the fly's weight *per second*! 25 m.p.h. is a more reasonable estimate. The naturalist should not forget, though it does not touch our present argument, that the aeroplane is built to the pattern of a beetle rather than of a bird; for the elytra are not wings but planes. Cf. *int. al.*, P. Amans, *Géométrie...des ailes rigides*, *C.R. Assoc. Franç. pour l'avancem. des Sc.* 1901.

observed phenomena. It tells us why the larger birds have a marked difficulty in rising from the ground, that is to say, in acquiring to begin with the horizontal velocity necessary for their support; and why accordingly, as Mouillard* and others have observed, the heavier birds, even those weighing no more than a pound or two, can be effectually caged in small enclosures open to the sky. It explains why, as Mr Abel Chapman says, "all ponderous birds, wild swans and geese, great bustard and capercailzie, even blackcock, fly faster than they appear to do," while "light-built types with a big wing-area†, such as herons and harriers, possess no turn of speed at all." For the fact is that the heavy birds must fly quickly, or not at all. It tells us why very small birds, especially those as small as humming-birds, and *à fortiori* the still smaller insects, are capable of "stationary flight," a very slight and scarcely perceptible velocity relatively to the air being sufficient for their support and stability. And again, since it is in all these cases velocity relatively to the air which we are speaking of, we comprehend the reason why one may always tell which way the wind blows by watching the direction in which a bird starts to fly.

The wing of a bird or insect, like the tail of a fish or the blade of an oar, gives rise at each impulsion to a swirl or vortex, which tends (so to speak) to cling to it and travel along with it; and the resistance which wing or oar encounter comes much more from these vortices than from the viscosity of the fluid.‡ We learn as a corollary to this, that vortices form only at the edge of oar or wing—it is only the length and not the breadth of these which matters. A long narrow oar outpaces a broad one, and the efficiency of the long, narrow wing of albatross, swift or hawkmoth is so far accounted for. From the length of the wing we can calculate approximately its rate of swing, and more conjecturally the dimensions of each vortex, and finally the resistance or lifting power of the stroke; and the result shews once again the advantages of the small-scale

* Mouillard, *L'empire de l'air; essai d'ornithologie appliquée à l'aviation*, 1881; transl. in *Annual Report of the Smithsonian Institution*, 1892.

† On wing-area in relation to weight of bird see Lendenfeld in *Naturw. Wochenschr.* Nov. 1904, transl. in *Smithsonian Inst. Rep.* 1904; also E. H. Hankin, *Animal Flight*, 1913; etc.

‡ Cf. V. Bjerknes, *Hydrodynamique physique*, II, p. 293, 1934.

mechanism, and the disadvantage under which the larger machine or larger creature lies.

	Weight gm.	Length of wing m.	Beats per sec.	Speed of wing-tip m./s.	Radius of vortex*	Force of wing-beat gm.	Specific force, <i>F/W</i>
(From V. Bjerkenes)							
Stork	3500	0.91	2	5.7	1.5	1480	2 : 5
Gull	1000	0.60	3	5.7	1.0	640	2 : 3
Pigeon	350	0.30	6	5.7	0.5	160	1 : 2
Sparrow	30	0.11	13	4.5	0.18	13	2 : 5
Bee	0.07	0.01	200	6.3	0.02	0.2	3½ : 1
Fly	0.01	0.007	190	4.2	0.01	0.04	4 : 1

* Conjectural.

A bird may exert a force at each stroke of its wing equal to one-half, let us say for safety one-quarter, of its own weight, more or less; but a bee or a fly does twice or thrice the equivalent of its own weight, at a low estimate. If stork, gull or pigeon can thus carry only one-fifth, one-third, one-quarter of their weight by the beating of their wings, it follows that all the rest must be borne by *sailing-flight* between the wing-beats. But an insect's wings lift it easily and with something to spare; hence sailing-flight, and with it the whole principle of necessary speed, does not concern the lesser insects, nor the smallest birds, at all; for a humming-bird can "stand still" in the air, like a hover-fly, and dart backwards as well as forwards, if it please.

There is a little group of Fairy-flies (*Mymaridae*), far below the size of any small familiar insects; their eggs are laid and larvae reared within the tiny eggs of larger insects; their bodies may be no more than $\frac{1}{2}$ mm. long, and their outspread wings 2 mm. from tip to tip (Fig. 2). It is a peculiarity of some of these that their little wings are made of a few hairs or bristles, instead of the continuous membrane of a wing. How these act on the minute quantity of air involved we can only conjecture. It would seem that that small quantity reacts as a viscous fluid to the beat of the wing; but there are doubtless other unobserved anomalies in the mechanism and the mode of flight of these pigmy creatures†.

The ostrich has apparently reached a magnitude, and the moa certainly did so, at which flight by muscular action, according to

† It is obvious that in a still smaller order of magnitude the Brownian movement would suffice to make flight impossible.

the normal anatomy of a bird, becomes physiologically impossible. The same reasoning applies to the case of man. It would be very difficult, and probably absolutely impossible, for a bird to flap its way through the air were it of the bigness of a man; but Borelli, in discussing the matter, laid even greater stress on the fact that a man's pectoral muscles are so much less in proportion than those of a bird, that however we might fit ourselves out with wings, we could never expect to flap them by any power of our own weak muscles. Borelli had learned this lesson thoroughly, and in one of his chapters he deals with the proposition: *Est impossibile ut homines propriis viribus artificiose volare possint**. But gliding flight, where



Fig. 2. Fairy-flies (*Mymaridae*): after F. Enock. $\times 20$.

wind-force and gravitational energy take the place of muscular power, is another story, and its limitations are of another kind. Nature has many modes and mechanisms of flight, in birds of one kind and another, in bats and beetles, butterflies, dragonflies and what not; and gliding seems to be the common way of birds, and the flapping flight (*remigio alarum*) of sparrow and of crow to be the exception rather than the rule. But it were truer to say that gliding and soaring, by which energy is captured from the wind, are modes of flight little needed by the small birds, but more and more essential to the large. Borelli had proved so convincingly that we could never hope to fly *propriis viribus*, that all through the eighteenth century men tried no more to fly at all. It was in trying to *glide* that the pioneers of aviation, Cayley, Wenham and Mouillard,

* Giovanni Alfonso Borelli, *De Motu Animalium*, 1, Prop. cciv, p. 243, edit. 1685. The part on *The Flight of Birds* is issued by the Royal Aeronautical Society as No. 6 of its *Aeronautical Classics*.

Langley, Lilienthal and the Wrights—all careful students of birds—renewed the attempt*; and only after the Wrights had learned to glide did they seek to add power to their glider. Flight, as the Wrights declared, is a matter of practice and of skill, and skill in gliding has now reached a point which more than justifies all Leonardo da Vinci's attempts to fly. Birds shew infinite skill and instinctive knowledge in the use they make of the horizontal acceleration of the wind, and the advantage they take of ascending currents in the air. Over the hot sands of the Sahara, where every here and there hot air is going up and cooler coming down, birds keep as best they can to the one, or glide quickly through the other; so we may watch a big dragonfly planing slowly down a few feet above the heated soil, and only every five minutes or so regaining height with a vigorous stroke of his wings. The albatross uses the upward current on the lee-side of a great ocean-wave; so, on a lesser scale, does the flying-fish; and the seagull flies in curves, taking every advantage of the varying wind-velocities at different levels over the sea. An Indian vulture flaps his way up for a few laborious yards, then catching an upward current soars in easy spirals to 2000 feet; here he may stay, effortless, all day long, and come down at sunset. Nor is the modern sail-plane much less efficient than a soaring bird; for a skilful pilot in the tropics should be able to roam all day long at will†.

A bird's sensitiveness to air-pressure is indicated in other ways besides. Heavy birds, like duck and partridge, fly low and apparently take advantage of air-pressure reflected from the ground. Water-hen and dipper follow the windings of the stream as they fly up or down; a bee-line would give them a shorter course, but not so smooth a journey. Some small birds—wagtails, woodpeckers and a few others—fly, so to speak, by leaps and bounds; they fly briskly

* Sir George Cayley (1774–1857), father of British aeronautics, was the first to perceive the capabilities of rigid planes, and to experiment on gliding flight. He anticipated all the essential principles of the modern aeroplane, and his first paper "On Aerial Navigation" appeared in *Nicholson's Journal* for November 1809. F. H. Wenham (1824–1908) studied the flight of birds and estimated the necessary proportion of surface to weight and speed; he held that "the whole secret of success in flight depends upon a proper concave form of the supporting surface." See his paper "On Aerial Locomotion" in the *Report of the Aeronautical Society* 1866.

† Sir Gilbert Walker, in *Nature*, Oct. 2, 1937.

for a few moments, then close their wings and shoot along*. The flying-fishes do much the same, save that they keep their wings outspread. The best of them "taxi" along with only their tails in the water, the tail vibrating with great rapidity, and the speed attained lasts the fish on its long glide through the air†.

Flying may have begun, as in Man's case it did, with short spells of gliding flight, helped by gravity, and far short of sustained or continuous locomotion. The short wings and long tail of Archaeopteryx would be efficient as a slow-speed glider; and we may still see a Touraco glide down from his perch looking not much unlike Archaeopteryx in the proportions of his wings and tail. The small bodies, scanty muscles and narrow but vastly elongated wings of a Pterodactyl go far beyond the limits of mechanical efficiency for ordinary flapping flight; but for gliding they approach perfection‡. Sooner or later Nature does everything which is physically possible; and to glide with skill and safety through the air is a possibility which she did not overlook.

Apart from all differences in the action of the limbs—apart from differences in mechanical construction or in the manner in which the mechanism is used—we have now arrived at a curiously simple and uniform result. For in all the three forms of locomotion which we have attempted to study, alike in swimming and in walking, and even in the more complex problem of flight, the general result, obtained under very different conditions and arrived at by different modes of reasoning, shews in every case that speed tends to vary as the square root of the linear dimensions of the animal.

While the rate of progress tends to increase slowly with increasing size (according to Froude's law), and the rhythm or pendulum-rate of the limbs to increase rapidly with decreasing size (according to Galileo's law), some such increase of velocity with decreasing

* Why large birds cannot do the same is discussed by Lanchester, *op. cit.* Appendix IV.

† Cf. Carl L. Hubbs, On the flight of...the Cypselurinae, and remarks on the evolution of the flight of fishes, *Papers of the Michigan Acad. of Sci.* xvii, pp. 575–611, 1933. See also E. H. Hankin, *P.Z.S.* 1920, pp. 467–474; and C. M. Breder, On the structural specialisation of flying fishes from the standpoint of aerodynamics, *Copeia*, 1930, pp. 114–121.

‡ The old conjecture that their flight was helped or rendered possible by a denser atmosphere than ours is thus no longer called for.

magnitude is true of all the rhythmic actions of the body, though for reasons not always easy to explain. The elephant's heart beats slower than ours*, the dog's quicker; the rabbit's goes pit-a-pat; the mouse's and the sparrow's are too quick to count. But the very "rate of living" (measured by the O consumed and CO₂ produced) slows down as size increases; and a rat lives so much faster than a man that the years of its life are three, instead of threescore and ten.

From all the foregoing discussion we learn that, as Crookes once upon a time remarked†, the forms as well as the actions of our bodies are entirely conditioned (save for certain exceptions in the case of aquatic animals) by the strength of gravity upon this globe; or, as Sir Charles Bell had put it some sixty years before, the very animals which move upon the surface of the earth are proportioned to its magnitude. Were the force of gravity to be doubled our bipedal form would be a failure, and the majority of terrestrial animals would resemble short-legged saurians, or else serpents. Birds and insects would suffer likewise, though with some compensation in the increased density of the air. On the other hand, if gravity were halved, we should get a lighter, slenderer, more active type, needing less energy, less heat, less heart, less lungs, less blood. Gravity not only controls the actions but also influences the forms of all save the least of organisms. The tree under its burden of leaves or fruit has changed its every curve and outline since its boughs were bare, and a mantle of snow will alter its configuration again. Sagging wrinkles, hanging breasts and many another sign of age are part of gravitation's slow relentless handiwork.

There are other physical factors besides gravity which help to limit the size to which an animal may grow and to define the conditions under which it may live. The small insects skating on a pool have their movements controlled and their freedom limited by the surface-tension between water and air, and the measure of that tension determines the magnitude which they may attain. A man coming wet from his bath carries a few ounces of water, and is perhaps 1 per cent. heavier than before; but a wet fly weighs twice as much as a dry one, and becomes a helpless thing. A small

* Say 28 to 30 beats to the minute.

† *Proc. Psychical Soc.* XII, p. 338-355, 1897.

insect finds itself imprisoned in a drop of water, and a fly with two feet in one drop finds it hard to extricate them.

The mechanical construction of insect or crustacean is highly efficient up to a certain size, but even crab and lobster never exceed certain moderate dimensions, perfect within these narrow bounds as their construction seems to be. Their body lies within a hollow shell, the stresses within which increase much faster than the mere scale of size; every hollow structure, every dome or cylinder, grows weaker as it grows larger, and a tin canister is easy to make but a great boiler is a complicated affair. The boiler has to be strengthened by "stiffening rings" or ridges, and so has the lobster's shell; but there is a limit even to this method of counteracting the weakening effect of size. An ordinary girder-bridge may be made efficient up to a span of 200 feet or so; but it is physically incapable of spanning the Firth of Forth. The great Japanese spider-crab, *Macrocheira*, has a span of some 12 feet across; but Nature meets the difficulty and solves the problem by keeping the body small, and building up the long and slender legs out of short lengths of narrow tubes. A hollow shell is admirable for small animals, but Nature does not and cannot make use of it for the large.

In the case of insects, other causes help to keep them of small dimensions. In their peculiar respiratory system blood does not carry oxygen to the tissues, but innumerable fine tubules or tracheae lead air into the interstices of the body. If we imagine them growing even to the size of crab or lobster, a vast complication of tracheal tubules would be necessary, within which friction would increase and diffusion be retarded, and which would soon be an inefficient and inappropriate mechanism.

The vibration of vocal chords and auditory drums has this in common with the pendulum-like motion of a limb that its rate also tends to vary inversely as the square root of the linear dimensions. We know by common experience of fiddle, drum or organ, that pitch rises, or the frequency of vibration increases, as the dimensions of pipe or membrane or string diminish; and in like manner we expect to hear a bass note from the great beasts and a piping treble from the small. The rate of vibration (N) of a stretched string depends on its tension and its density; these being equal, it varies inversely as its own length and as its diameter. For similar

strings, $N \propto 1/l^2$, and for a circular membrane, of radius r and thickness e , $N \propto 1/(r^2 \sqrt{e})$.

But the delicate drums or tympana of various animals seem to vary much less in thickness than in diameter, and we may be content to write, once more, $N \propto 1/r^2$.

Suppose one animal to be fifty times less than another, vocal chords and all: the one's voice will be pitched 2500 times as many beats, or some ten or eleven octaves, above the other's; and the same comparison, or the same contrast, will apply to the tympanic membranes by which the vibrations are received. But our own perception of musical notes only reaches to 4000 vibrations per second, or thereby; a squeaking mouse or bat is heard by few, and to vibrations of 10,000 per second we are all of us stone-deaf. Structure apart, mere size is enough to give the lesser birds and beasts a music quite different to our own: the humming-bird, for aught we know, may be singing all day long. A minute insect may utter and receive vibrations of prodigious rapidity; even its little wings may beat hundreds of times a second*. Far more things happen to it in a second than to us; a thousandth part of a second is no longer negligible, and time itself seems to run a different course to ours.

The eye and its retinal elements have ranges of magnitude and limitations of magnitude of their own. A big dog's eye is hardly bigger than a little dog's; a squirrel's is much larger, proportionately, than an elephant's; and a robin's is but little less than a pigeon's or a crow's. For the rods and cones do not vary with the size of the animal, but have their dimensions optically limited by the interference-patterns of the waves of light, which set bounds to the production of clear retinal images. True, the larger animal may want a larger field of view; but this makes little difference, for but a small area of the retina is ever needed or used. The eye, in short, can never be very small and need never be very big; it has its own conditions and limitations apart from the size of the animal. But the insect's eye tells another story. If a fly had an eye like ours, the pupil would be so small that diffraction would render a clear image impossible. The only alternative is to unite a number

* The wing-beats are said to be as follows: dragonfly 28 per sec., bee 190, housefly 330; cf. Erhard, *Deutsche Zool. ges. Verh.* 1913, p. 206.

of small and optically isolated simple eyes into a compound eye, and in the insect Nature adopts this alternative possibility*.

Our range of vision is limited to a bare octave of "luminous" waves, which is a considerable part of the whole range of light-heat rays emitted by the sun; the sun's rays extend into the ultra-violet for another half-octave or more, but the rays to which our eyes are sensitive are just those which pass with the least absorption through a watery medium. Some ancient vertebrate may have learned to see in an ocean which let a certain part of the sun's whole radiation through, which part is *our part* still; or perhaps the watery media of the eye itself account sufficiently for the selective filtration. In either case, the dimensions of the retinal elements are so closely related to the wave-lengths of light (or to their interference patterns) that we have good reason to look upon the retina as perfect of its kind, within the limits which the properties of light itself impose; and this perfection is further illustrated by the fact that a few light-quanta, perhaps a single one, suffice to produce a sensation†. The hard eyes of insects are sensitive over a wider range. The bee has two visual optima, one coincident with our own, the other and principal one high up in the ultra-violet‡. And with the latter the bee is able to see that ultra-violet which is so well reflected by many flowers that flower-photographs have been taken through a filter which passes these but transmits no other rays§.

When we talk of light, and of magnitudes whose order is that of a wave-length of light, the subtle phenomenon of colour is near at hand. The hues of living things are due to sundry causes; where they come from chemical pigmentation they are outside our theme, but oftentimes there is no pigment at all, save perhaps as a screen or background, and the tints are those proper to a scale of wave-lengths or range of magnitude. In birds these "optical colours" are of two chief kinds. One kind include certain vivid blues, the

* Cf. C. J. van der Horst, The optics of the insect eye, *Acta Zoolog.* 1933, p. 108.

† Cf. Niels Bohr, in *Nature*, April 1, 1933, p. 457. Also J. Joly, *Proc. R.S. (B)*, xcii, p. 222, 1921.

‡ L. M. Bertholf, Reactions of the honey-bee to light, *Journ. of Agric. Res.* xlvi, p. 379; xliv, p. 763, 1931.

§ A. Kuhn, Ueber den Farbensinn der Bienen, *Ztschr. d. vergl. Physiol.* v, pp. 762-800, 1927; cf. F. K. Richtmeyer, Reflection of ultra-violet by flowers, *Journ. Optical Soc. Amer.* vii, pp. 151-168, 1923; etc.

blue of a blue jay, an Indian roller or a macaw; to the other belong the iridescent hues of mother-of-pearl, of the humming-bird, the peacock and the dove: for the dove's grey breast shews many colours yet contains but one—*colores inesse plures nec esse plus uno*, as Cicero said. The jay's blue feather shews a layer of enamel-like cells beneath a thin horny cuticle, and the cell-walls are spongy with innumerable tiny air-filled pores. These are about 0.3μ in diameter, in some birds even a little less, and so are not far from the limits of microscopic vision. A deeper layer carries dark-brown pigment, but there is no blue pigment at all; if the feather be dipped in a fluid of refractive index equal to its own, the blue utterly disappears, to reappear when the feather dries. This blue is like the colour of the sky; it is "Tyndall's blue," such as is displayed by turbid media, cloudy with dust-motes or tiny bubbles of a size comparable to the wave-lengths of the blue end of the spectrum. The longer waves of red or yellow pass through, the shorter violet rays are reflected or scattered; the intensity of the blue depends on the size and concentration of the particles, while the dark pigment-screen enhances the effect.

Rainbow hues are more subtle and more complicated; but in the peacock and the humming-bird we know for certain* that the colours are those of Newton's rings, and are produced by thin plates or films covering the barbules of the feather. The colours are such as are shewn by films about $\frac{1}{2}\mu$ thick, more or less; they change towards the blue end of the spectrum as the light falls more and more obliquely; or towards the red end if you soak the feather and cause the thin plates to swell. The barbules of the peacock's feather are broad and flat, smooth and shiny, and their cuticular layer splits into three very thin transparent films, hardly more than 1μ thick, all three together. The gorgeous tints of the humming-birds have had their places in Newton's scale-defined, and the changes which they exhibit at varying incidence have been predicted

* Rayleigh, *Phil. Mag.* (6), xxxvii, p. 98, 1919. For a review of the whole subject, and a discussion of its many difficulties, see H. Onslow, On a periodic structure in many insect scales, etc., *Phil. Trans. (B)*, ccxi, pp. 1-74, 1921; also C. W. Mason, *Journ. Physic. Chemistry*, xxvii, xxx, xxxi, 1923-25-27; F. Suffert, *Zeitschr. f. Morph. u. Oekol. d. Tiere*, i, pp. 171-306, 1924 (scales of butterflies); also B. Reusch and Th. Elsasser in *Journ. f. Ornithologie*, lxxiii, 1925; etc.

and explained. The thickness of each film lies on the very limit of microscopic vision, and the least change or irregularity in this minute dimension would throw the whole display of colour out of gear. No phenomenon of organic magnitude is more striking than this constancy of size; none more remarkable than that these fine lamellae should have their tenuity so sharply defined, so uniform in feather after feather, so identical in all the individuals of a species, so constant from one generation to another.

A simpler phenomenon, and one which is visible throughout the whole field of morphology, is the tendency (referable doubtless in each case to some definite physical cause) for mere bodily *surface* to keep pace with *volume*, through some alteration of its form. The development of villi on the lining of the intestine (which increase its surface much as we enlarge the effective surface of a bath-towel), the various valvular folds of the intestinal lining, including the remarkable "spiral valve" of the shark's gut, the lobulation of the kidney in large animals*, the vast increase of respiratory surface in the air-sacs and alveoli of the lung, the development of gills in the larger crustacea and worms though the general surface of the body suffices for respiration in the smaller species—all these and many more are cases in which a more or less constant ratio tends to be maintained between mass and surface, which ratio would have been more and more departed from with increasing size, had it not been for such alteration of surface-form†. A leafy wood, a grassy sward, a piece of sponge, a reef of coral, are all instances of a like phenomenon. In fact, a deal of evolution is involved in keeping due balance between surface and mass as growth goes on.

In the case of very small animals, and of individual cells, the principle becomes especially important, in consequence of the molecular forces whose resultant action is limited to the superficial layer. In the cases just mentioned, action is *facilitated* by increase of surface: diffusion, for instance, of nutrient liquids or respiratory gases is rendered more rapid by the greater area of surface; but

* Cf. R. Anthony, *C.R. CLXIX*, p. 1174, 1919, etc. Cf. also A. Pütter, *Studien über physiologische Ähnlichkeit*, *Pflüger's Archiv*, CLXVIII, pp. 209–246, 1917.

† For various calculations of the increase of surface due to histological and anatomical subdivision, see E. Babak, *Ueber die Oberflächenentwicklung bei Organismen*, *Biol. Centralbl.* xxx, pp. 225–239, 257–267, 1910.

there are other cases in which the ratio of surface to mass may change the whole condition of the system. Iron rusts when exposed to moist air, but it rusts ever so much faster, and is soon eaten away, if the iron be first reduced to a heap of small filings; this is a mere difference of degree. But the spherical surface of the rain-drop and the spherical surface of the ocean (though both happen to be alike in mathematical form) are two totally different phenomena, the one due to surface-energy, and the other to that form of mass-energy which we ascribe to gravity. The contrast is still more clearly seen in the case of waves: for the little ripple, whose form and manner of propagation are governed by surface-tension, is found to travel with a velocity which is inversely as the square root of its length; while the ordinary big waves, controlled by gravitation, have a velocity directly proportional to the square root of their wave-length. In like manner we shall find that the form of all very small organisms is independent of gravity, and largely if not mainly due to the force of surface-tension: either as the direct result of the continued action of surface-tension on the semi-fluid body, or else as the result of its action at a prior stage of development, in bringing about a form which subsequent chemical changes have rendered rigid and lasting. In either case, we shall find a great tendency in small organisms to assume either the spherical form or other simple forms related to ordinary inanimate surface-tension phenomena, which forms do not recur in the external morphology of large animals.

Now this is a very important matter, and is a notable illustration of that principle of similitude which we have already discussed in regard to several of its manifestations. We are coming to a conclusion which will affect the whole course of our argument throughout this book, namely that there is an essential difference in kind between the phenomena of form in the larger and the smaller organisms. I have called this book a study of *Growth and Form*, because in the most familiar illustrations of organic form, as in our own bodies for example, these two factors are inseparably associated, and because we are here justified in thinking of form as the direct resultant and consequence of growth: of growth, whose varying rate in one direction or another has produced, by its gradual and unequal increments, the successive stages of development and

the final configuration of the whole material structure. But it is by no means true that form and growth are in this direct and simple fashion correlative or complementary in the case of minute portions of living matter. For in the smaller organisms, and in the individual cells of the larger, we have reached an order of magnitude in which the intermolecular forces strive under favourable conditions with, and at length altogether outweigh, the force of gravity, and also those other forces leading to movements of convection which are the prevailing factors in the larger material aggregate.

However, we shall require to deal more fully with this matter in our discussion of the rate of growth, and we may leave it meanwhile, in order to deal with other matters more or less directly concerned with the magnitude of the cell.

The living cell is a very complex field of energy, and of energy of many kinds, of which surface-energy is not the least. Now the whole surface-energy of the cell is by no means restricted to its outer surface; for the cell is a very heterogeneous structure, and all its protoplasmic alveoli and other visible (as well as invisible) heterogeneities make up a great system of internal surfaces, at every part of which one "phase" comes in contact with another "phase," and surface-energy is manifested accordingly. But still, the external surface is a definite portion of the system, with a definite "phase" of its own, and however little we may know of the distribution of the total energy of the system, it is at least plain that the conditions which favour equilibrium will be greatly altered by the changed ratio of external surface to mass which a mere change of magnitude produces in the cell. In short, the phenomenon of division of the growing cell, however it be brought about, will be precisely what is wanted to keep fairly constant the ratio between surface and mass, and to retain or restore the balance between surface-energy and the other forces of the system*. But when a germ-cell divides or "segments" into two, it does not increase in mass; at least if there be some slight alleged tendency for the egg to increase in

* Certain cells of the cucumber were found to divide when they had grown to a volume half as large again as that of the "resting cells." Thus the volumes of resting, dividing and daughter cells were as 1 : 1.5 : 0.75; and their surfaces, being as the power $2/3$ of these figures, were, roughly, as 1 : 1.3 : 0.8. The ratio of S/V was then as 1 : 0.9 : 1.1, or much nearer equality. Cf. F. T. Lewis, *Anat. Record*, XLVII, pp. 59–99, 1930.

mass or volume during segmentation it is very slight indeed, generally imperceptible, and wholly denied by some*. The growth or development of the egg from a one-celled stage to stages of two or many cells is thus a somewhat peculiar kind of growth; it is growth limited to change of form and increase of surface, unaccompanied by growth in volume or in mass. In the case of a soap-bubble, by the way, if it divide into two bubbles the volume is actually diminished, while the surface-area is greatly increased†; the diminution being due to a cause which we shall have to study later, namely to the increased pressure due to the greater curvature of the smaller bubbles.

An immediate and remarkable result of the principles just described is a tendency on the part of all cells, according to their kind, to vary but little about a certain mean size, and to have in fact certain absolute limitations of magnitude. The diameter of a large parenchymatous cell is perhaps tenfold that of a little one; but the tallest phanerogams are ten thousand times the height of the least. In short, Nature has her materials of predeterminate dimensions, and keeps to the same bricks whether she build a great house or a small. Even ordinary drops tend towards a certain fixed size, which size is a function of the surface-tension, and may be used (as Quincke used it) as a measure thereof. In a shower of rain the principle is curiously illustrated, as Wilding Kölle and V. Bjerknes tell us. The drops are of graded sizes, *each twice as big as another*, beginning with the minute and uniform droplets of an impalpable mist. They rotate as they fall, and if two rotate in contrary directions they draw together and presently coalesce; but this only happens when two drops are falling side by side, and since the rate of fall depends on the size it always is a pair of coequal drops which so meet, approach and join together. A supreme instance of constancy or quasi-constancy of size, remote from but yet analogous to the size-limitation of a rain-drop or a cell, is the fact that the stars of heaven (however else one differeth from another), and even the nebulae themselves, are all wellnigh co-equal in *mass*. Gravity draws matter together, condensing it into a world

* Though the entire egg is not increasing in mass, that is not to say that its living protoplasm is not increasing all the while at the expense of the reserve material.

† Cf. P. G. Tait, *Proc. R.S.E.* v, 1866 and vi, 1868.

or into a star; but ethereal pressure is an opponent force leading to disruption, negligible on the small scale but potent on the large. High up in the scale of magnitude, from about 10^{33} to 10^{35} grams of matter, these two great cosmic forces balance one another; and all the magnitudes of all the stars lie within or hard by these narrow limits.

In the living cell, Sachs pointed out (in 1895) that there is a tendency for each nucleus to gather around itself a certain definite amount of protoplasm*. Driesch†, a little later, found it possible, by artificial subdivision of the egg, to rear dwarf sea-urchin larvae, one-half, one-quarter or even one-eighth of their usual size; which dwarf larvae were composed of only a half, a quarter or an eighth of the normal number of cells. These observations have been often repeated and amply confirmed: and Loeb found the sea-urchin eggs capable of reduction to a certain size, but no further.

In the development of *Crepidula* (an American "slipper-limpet," now much at home on our oyster-beds), Conklin‡ has succeeded in rearing dwarf and giant individuals, of which the latter may be five-and-twenty times as big as the former. But the individual cells, of skin, gut, liver, muscle and other tissues, are just the same size in one as in the other, in dwarf and in giant§. In like manner

* *Physiologische Notizen* (9), p. 425, 1895. Cf. Amelung, *Flora*, 1893; Strasburger, Ueber die Wirkungssphäre der Kerne und die Zellgrösse, *Histol. Beitr.* (5), pp. 95-129, 1893; R. Hertwig, Ueber Korrelation von Zell- und Kerngrösse (Kernplasmarelation), *Biol. Centralbl.* xviii, pp. 49-62, 108-119, 1903; G. Levi and T. Terni, Le variazioni dell' indice plasmatico-nucleare durante l' intercinesi, *Arch. Ital. di Anat.* x, p. 545, 1911; also E. le Breton and G. Schaeffer, *Variations biochimiques du rapport nucléo-plasmique*, Strasburg, 1923.

† *Arch. f. Entw. Mech.* iv, 1898, pp. 75, 247.

‡ E. G. Conklin, Cell-size and nuclear size, *Journ. Exp. Zool.* xii, pp. 1-98, 1912; Body-size and cell-size, *Journ. of Morphol.* xxiii, pp. 159-188, 1912. Cf. M. Popoff, Ueber die Zellgrösse, *Arch. f. Zellforschung*, iii, 1909.

§ Thus the fibres of the crystalline lens are of the same size in large and small dogs, Rabl, *Z. f. w. Z.* Lxvii, 1899. Cf. (*int. al.*) Pearson, On the size of the blood-corpuscles in *Rana*, *Biometrika*, vi, p. 403, 1909. Dr Thomas Young caught sight of the phenomenon early in last century: "The solid particles of the blood do not by any means vary in magnitude in the same ratio with the bulk of the animal," *Natural Philosophy*, ed. 1845, p. 466; and Leeuwenhoek and Stephen Hales were aware of it nearly two hundred years before. Leeuwenhoek indeed had a very good idea of the size of a human blood-corpuscle, and was in the habit of using its diameter—about $1/3000$ of an inch—as a standard of comparison. But though the blood-corpuscles shew no relation of magnitude to the size of the animal, they are related without doubt to its activity; for the corpuscles in the

the leaf-cells are found to be of the same size in an ordinary water-lily, in the great *Victoria regia*, and in the still huger leaf, nearly 3 metres long, of *Euryale ferox* in Japan*. Driesch has laid particular stress upon this principle of a "fixed cell-size," which has, however, its own limitations and exceptions. Among these exceptions, or apparent exceptions, are the giant frond-like cell of a Caulerpa or the great undivided plasmodium of a Myxomycete. The flattening of the one and the branching of the other serve (or help) to increase the ratio of surface to content, the nuclei tend to multiply, and streaming currents keep the interior and exterior of the mass in touch with one another.

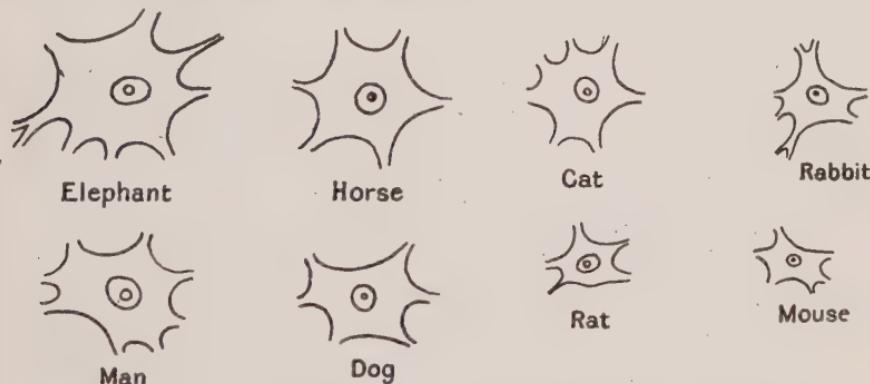


Fig. 3. Motor ganglion-cells, from the cervical spinal cord.
From Minot, after Irving Hardesty.

We get a good and even a familiar illustration of the principle of size-limitation in comparing the brain-cells or ganglion-cells, whether of the lower or of the higher animals†. In Fig. 3 we shew certain identical nerve-cells from various mammals, from mouse to elephant, all drawn to the same scale of magnification; and we see that they are all of much the same *order* of magnitude. The nerve-cell of the elephant is about twice that of the mouse in linear

sluggish Amphibia are much the largest known to us, while the smallest are found among the deer and other agile and speedy animals (cf. Gulliver, *P.Z.S.* 1875, p. 474, etc.). This correlation is explained by the surface condensation or adsorption of oxygen in the blood-corpuscles, a process greatly facilitated and intensified by the increase of surface due to their minuteness.

* Okada and Yomosuke, in *Sci. Rep. Tohoku Univ.* III, pp. 271-278, 1928.

† Cf. P. Enriques, La forma come funzione della grandezza: Ricerche sui gangli nervosi degli invertebrati, *Arch. f. Entw. Mech.* xxv, p. 655, 1907-8.

dimensions, and therefore about eight times greater in volume or in mass. But making due allowance for difference of shape, the linear dimensions of the elephant are to those of the mouse as not less than one to fifty; and the bulk of the larger animal is something like 125,000 times that of the less. It follows, if the size of the nerve-cells are as eight to one, that, in corresponding parts of the nervous system, there are more than 15,000 times as many individual cells in one animal as in the other. In short we may (with Enriques) lay it down as a general law that among animals, large or small, the ganglion-cells vary in size within narrow limits; and that, amidst all the great variety of structure observed in the nervous system of different classes of animals, it is always found that the smaller species have simpler ganglia than the larger, that is to say ganglia containing a smaller number of cellular elements*. The bearing of such facts as this upon the cell-theory in general is not to be disregarded; and the warning is especially clear against exaggerated attempts to correlate physiological processes with the visible mechanism of associated cells, rather than with the system of energies, or the field of force, which is associated with them. For the life of the body is more than the *sum* of the properties of the cells of which it is composed: as Goethe said, "Das Lebendige ist zwar in Elemente zerlegt, aber man kann es aus diesen nicht wieder zusammenstellen und beleben."

Among certain microscopic organisms such as the Rotifera (which have the least average size and the narrowest range of size of all the Metazoa), we are still more palpably struck by the small number of cells which go to constitute a usually complex organ, such as kidney, stomach or ovary; we can sometimes number them in a few

* While the difference in cell-volume is vastly less than that between the volumes, and very much less also than that between the surfaces, of the respective animals, yet there *is* a certain difference; and this it has been attempted to correlate with the need for each cell in the many-celled ganglion of the larger animal to possess a more complex "exchange-system" of branches, for intercommunication with its more numerous neighbours. Another explanation is based on the fact that, while such cells as continue to divide throughout life tend to uniformity of size in all mammals, those which do not do so, and in particular the ganglion cells, continue to grow, and their size becomes, therefore, a function of the duration of life. Cf. G. Levi, Studii sulla grandezza delle cellule, *Arch. Ital. di Anat. e di Embriolog.* v, p. 291, 1906; cf. also A. Berezowski, Studien über die Zellgrösse, *Arch. f. Zellforsch.* v, pp. 375-384, 1910.

units, in place of the many thousands which make up such an organ in larger, if not always higher, animals. We have already spoken of the Fairy-flies, a few score of which would hardly weigh down one of the larger rotifers, and a hundred thousand would weigh less than one honey-bee. Their form is complex and their little bodies exquisitely beautiful; but I feel sure that their cells are few, and their organs of great histological simplicity. These considerations help, I think, to shew that, however important and advantageous the subdivision of the tissues into cells may be from the constructional, or from the dynamic, point of view, the phenomenon has less fundamental importance than was once, and is often still, assigned to it.

Just as Sachs shewed there was a limit to the amount of cytoplasm which could gather round a nucleus, so Boveri has demonstrated that the nucleus itself has its own limitations of size, and that, in cell-division after fertilisation, each new nucleus has the same size as its parent nucleus*; we may nowadays transfer the statement to the chromosomes. It may be that a bacterium lacks a nucleus for the simple reason that it is too small to hold one, and that the same is true of such small plants as the Cyanophyceae, or blue-green algae. Even a chromatophore with its "pyrenoids" seems to be impossible below a certain size†.

Always then, there are reasons, partly physiological but in large part purely physical, which define or regulate the magnitude of the organism or the cell. And as we have already found definite limitations to the increase in magnitude of an organism, let us now enquire whether there be not also a lower limit below which the very existence of an organism becomes impossible.

* Boveri, *Zellenstudien*, V: Ueber die Abhängigkeit der Kerngrösse und Zellenzahl von der Chromosomenzahl der Ausgangszellen. Jena, 1905. Cf. also (*int. al.*) H. Voss, Kerngrößenverhältnisse in der Leber etc., *Ztschr. f. Zellforschung*, VII, pp. 187–200, 1928.

† The size of the nucleus may be affected, even determined, by the number of chromosomes it contains. There are giant races of *Oenothera*, *Primula* and *Solanum* whose cell-nuclei contain twice the normal number of chromosomes, and a dwarf race of a little freshwater crustacean, *Cyclops*, has half the usual number. The cytoplasm in turn varies with the amount of nuclear matter, the whole cell is unusually large or unusually small; and in these exceptional cases we see a direct relation between the size of the organism and the size of the cell. Cf. (*int. al.*) R. P. Gregory, *Proc. Camb. Phil. Soc.* xv, pp. 239–246, 1909; F. Keeble, *Journ. of Genetics*, II, pp. 163–188, 1912.

A bacillus of ordinary size is, say, 1μ in length. The length (or height) of a man is about a million and three-quarter times as great, i.e. 1.75 metres, or $1.75 \times 10^6\mu$; and the mass of the man is in the neighbourhood of 5×10^{18} (five million, million, million) times greater than that of the bacillus. If we ask whether there may not exist organisms as much less than the bacillus as the bacillus is less than the man, it is easy to reply that this is quite impossible, for we are rapidly approaching a point where the question of molecular dimensions, and of the ultimate divisibility of matter, obtrudes itself as a crucial factor in the case. Clerk Maxwell dealt with this matter seventy years ago, in his celebrated article *Atom**. Kolli (or Colley), a Russian chemist, declared in 1893 that the head of a spermatozoon could hold no more than a few protein molecules; and Errera, ten years later, discussed the same topic with great ingenuity†. But it needs no elaborate calculation to convince us that the smaller bacteria or micrococci nearly approach the smallest magnitudes which we can conceive to have an organised structure. A few small bacteria are the smallest of visible organisms, and a minute species associated with influenza, *B. pneumosinter*, is said to be the least of them all. Its size is of the order of 0.1μ , or rather less; and here we are in close touch with the utmost limits of microscopic vision, for the wave-lengths of visible light run only from about 400 to $700\text{ m}\mu$. The largest of the bacteria, *B. megatherium*, larger than the well-known *B. anthracis* of splenic fever, has much the same proportion to the least as an elephant to a guinea-pig‡.

Size of body is no mere accident. Man, respiring as he does, cannot be as small as an insect, nor *vice versa*; only now and then, as in the Goliath beetle, do the sizes of mouse and beetle meet and overlap. The descending scale of mammals stops short at a weight of about 5 grams, that of beetles at a length of about half a millimetre, and every group of animals has its upper and its lower limitations of size. So, not far from the lower limit of our vision, does the long series of bacteria come to an end. There remain still smaller particles which the ultra-microscope in part reveals; and

* *Encyclopaedia Britannica*, 9th edition, 1875.

† Leo Errera, Sur la limite de la petitesse des organismes, *Bull. Soc. Roy. des Sc. méd. et nat. de Bruxelles*, 1903; *Recueil d'œuvres (Physiologie générale)*, p. 325.

‡ Cf. A. E. Boycott, The transition from live to dead, *Proc. R. Soc. of Medicine*, xxii (*Pathology*), pp. 55-69, 1928.

here or hereabouts are said to come the so-called viruses or "filter-passers," brought within our ken by the maladies, such as hydrophobia, or foot-and-mouth disease, or the mosaic diseases of tobacco and potato, to which they give rise. These minute particles, of the order of one-tenth the diameter of our smallest bacteria, have no diffusible contents, no included water—whereby they differ from every living thing. They appear to be inert colloidal (or even crystallloid) aggregates of a nucleo-protein, of perhaps ten times the diameter of an ordinary protein-molecule, and not much larger than the giant molecules of haemoglobin or haemocyanin*.

Beijerinck called such a virus a *contagium vivum*; "infective nucleo-protein" is a newer name. We have stepped down, by a single step, from living to non-living things, from bacterial dimensions to the molecular magnitudes of protein chemistry. And we begin to suspect that the virus-diseases are not due to an "organism, capable of physiological reproduction and multiplication, but to a mere specific chemical substance, capable of catalysing pre-existing materials and thereby producing more and more molecules like itself. The spread of the virus in a plant would then be a mere autocatalysis, not involving the transport of matter, but only a progressive change of state in substances already there†."

But, after all, a simple tabulation is all we need to shew how nearly the least of organisms approach to molecular magnitudes. The same table will suffice to shew how each main group of animals has its mean and characteristic size, and a range on either side, sometimes greater and sometimes less.

Our table of magnitudes is no mere catalogue of isolated facts, but goes deep into the relation between the creature and its world. A certain range, and a narrow one, contains mouse and elephant, and all whose business it is to walk and run; this is our own world,

* Cf. Svedberg, *Journ. Am. Chem. Soc.* XLVIII, p. 30, 1926. According to the Foot-and-Mouth Disease Research Committee (*5th Report*, 1937), the foot-and-mouth virus has a diameter, determined by graded filters, of 8-12 m μ ; while Kenneth Smith and W. D. MacClement (*Proc. R.S. (B)*, cxxv, p. 296, 1938) calculate for certain others a diameter of no more than 4 m μ , or less than a molecule of haemocyanin.

† H. H. Dixon, Croonian lecture on the transport of substances in plants, *Proc. R.S. (B)*, vol. cxxv, pp. 22, 23, 1938.

with whose dimensions our lives, our limbs, our senses are in tune. The great whales grow out of this range by throwing the burden of their bulk upon the waters; the dinosaurs wallowed in the swamp, and the hippopotamus, the sea-elephant and Steller's great sea-cow pass or passed their lives in the rivers or the sea. The things which

Linear dimensions of organisms, and other objects

	cm.	
(10,000 km.)	10^7	A quadrant of the earth's circumference
(1000 km.)	10^6	Orkney to Land's End
	10^5	
	10^4	Mount Everest
(km.)	10^3	
	10^2	Giant trees: <i>Sequoia</i>
		Large whale
	10^1	Basking shark
		Elephant; ostrich; man
(metre)	10^0	
	10^{-1}	Dog; rat; eagle
(cm.)	10^{-2}	Small birds and mammals; large insects
(mm.)	10^{-3}	Small insects; minute fish
	10^{-4}	Minute insects
	10^{-5}	Protozoa; pollen-grains
(micron, μ)	10^{-6}	Large bacteria; human blood-corpuscles
	10^{-7}	Minute bacteria
		Limit of microscopic vision
	10^{-8}	Viruses, or filter-passers
		Giant albuminoids, casein, etc. } Colloid particles
(m μ)	10^{-9}	Starch-molecule
(Ångström unit)	10^{-10}	Water-molecule

fly are smaller than the things which walk and run; the flying birds are never as large as the larger mammals, the lesser birds and mammals are much of a muchness, but insects come down a step in the scale and more. The lessening influence of gravity facilitates flight, but makes it less easy to walk and run; first claws, then hooks and suckers and glandular hairs help to secure a foothold,

until to creep upon wall or ceiling becomes as easy as to walk upon the ground. Fishes, by evading gravity, increase their range of magnitude both above and below that of terrestrial animals. Smaller than all these, passing out of our range of vision and going down to the least dimensions of living things, are protozoa, rotifers, spores, pollen-grains* and bacteria. All save the largest of these float rather than swim; they are buoyed up by air or water, and fall (as Stokes's law explains) with exceeding slowness.

There is a certain narrow range of magnitudes where (as we have partly said) gravity and surface tension become comparable forces, nicely balanced with one another. Here a population of small plants and animals not only dwell in the surface waters but are bound to the surface film itself—the whirligig beetles and pond-skaters, the larvae of gnat and mosquito, the duckweeds (*Lemna*), the tiny *Wolffia*, and *Azolla*; even in mid-ocean, one small insect (*Halobates*) retains this singular habitat. It would be a long story to tell the various ways in which surface-tension is thus taken full advantage of. Gravitation not only limits the magnitude but controls the form of things. With the help of gravity the quadruped has its back and its belly, and its limbs upon the ground; its freedom of motion in a plane perpendicular to gravitational force; its sense of fore-and-aft, its head and tail, its bilateral symmetry. Gravitation influences both our bodies and our minds. We owe to it our sense of the vertical, our knowledge of up-and-down; our conception of the horizontal plane on which we stand, and our discovery of two axes therein, related to the vertical as to one another; it was gravity which taught us to think of three-dimensional space. Our architecture is controlled by gravity, but gravity has less influence over the architecture of the bee; a bee might be excused, might even be commended, if it referred space to four dimensions instead of three!† The plant has its root and its stem; but about this vertical or

* Pollen-grains, like protozoa, have a considerable range of magnitude. The largest, such as those of the pumpkin, are about 200μ in diameter; these have to be carried by insects, for they are above the level of Stokes's law, and no longer float upon the air. The smallest pollen-grains, such as those of the forget-me-not, are about $4\frac{1}{2}\mu$ in diameter (Wodehouse).

† Corresponding, that is to say, to the four axes which, meeting in a point, make co-equal angles (the so-called tetrahedral angles) one with another, as do the basal angles of the honeycomb. (See below, chap. vii.)

gravitational axis its radiate symmetry remains, undisturbed by directional polarity, save for the sun. Among animals, radiate symmetry is confined to creatures of no great size; and some form or degree of spherical symmetry becomes the rule in the small world of the protozoon—unless gravity resume its sway through the added burden of a shell. The creatures which swim, walk or run, fly, creep or float are, so to speak, inhabitants and natural proprietors of as many distinct and all but separate worlds. Humming-bird and hawkmoth may, once in a way, be co-tenants of the same world; but for the most part the mammal, the bird, the fish, the insect and the small life of the sea, not only have their zoological distinctions, but each has a physical universe of its own. The world of bacteria is yet another world again, and so is the world of colloids; but through these small Lilliputs we pass outside the range of living things.

What we call mechanical principles apply to the magnitudes among which we are at home; but lesser worlds are governed by other and appropriate physical laws, of capillarity, adsorption and electric charge. There are other worlds at the far other end of the scale, in the uttermost depths of space, whose vast magnitudes lie within a narrow range. When the globular star-clusters are plotted on a curve, apparent diameter against estimated distance, the curve is a fair approximation to a rectangular hyperbola; which means that, to the same rough approximation, the actual diameter is identical in them all*.

It is a remarkable thing, worth pausing to reflect on, that we can pass so easily and in a dozen lines from molecular magnitudes† to the dimensions of a Sequoia or a whale. Addition and subtraction, the old arithmetic of the Egyptians, are not powerful enough for such an operation; but the story of the grains of wheat upon the chessboard shewed the way, and Archimedes and Napier elaborated

* See Harlow Shapley and A. B. Sayer, The angular diameters of globular clusters, *Proc. Nat. Acad. of Sci.* xxi, pp. 593–597, 1935. The same is approximately true of the spiral nebulae also.

† We may call (after Siedentopf and Zsigmondi) the smallest visible particles *microns*, such for instance as small bacteria, or the fine particles of gum-mastich in suspension, measuring 0.5 to $1.0\text{ }\mu$; *sub-microns* are those revealed by the ultra-microscope, such as particles of colloid gold (2 – $15\text{ m}\mu$), or starch-molecules ($5\text{ m}\mu$); *amicrons*, under $1\text{ m}\mu$, are not perceptible by either method. A water-molecule measures, probably, about $0.1\text{ m}\mu$.

the arithmetic of multiplication. So passing up and down by easy steps, as Archimedes did when he numbered the sands of the sea, we compare the magnitudes of the great beasts and the small, of the atoms of which they are made, and of the world in which they dwell*.

While considerations based on the chemical composition of the organism have taught us that there must be a definite lower limit to its magnitude, other considerations of a purely physical kind lead us to the same conclusion. For our discussion of the principle of similitude has already taught us that long before we reach these all but infinitesimal magnitudes the dwindling organism will have experienced great changes in all its physical relations, and must at length arrive at conditions surely incompatible with life, or what we understand as life, in its ordinary development and manifestation.

We are told, for instance, that the powerful force of surface-tension, or capillarity, begins to act within a range of about 1/500,000 of an inch, or say $0\cdot05\mu$. A soap film, or a film of oil on water, may be attenuated to far less magnitudes than this; the black spots on a soap bubble are known, by various concordant methods of measurement, to be only about 6×10^{-7} cm., or about $6m\mu$ thick, and Lord Rayleigh and M. Devaux have obtained films of oil of $2m\mu$, or even $1m\mu$ in thickness. But while it is possible for a fluid film to exist of these molecular dimensions, it is certain that long before we reach these magnitudes there arise conditions of which we have little knowledge, and which it is not easy to imagine. A bacillus lives in a world, or on the borders of a world, far other than our own, and preconceptions drawn from our experience are not valid there. Even among inorganic, non-living bodies, there comes a certain grade of minuteness at which the ordinary properties become modified. For instance, while under ordinary circumstances crystallisation starts in a solution about a minute solid fragment or crystal

* Observe that, following a common custom, we have only used a logarithmic scale for the round numbers representing powers of ten, leaving the interspaces between these to be filled up, if at all, by ordinary numbers. There is nothing to prevent us from using fractional indices, if we please, throughout, and calling a blood-corpuscle, for instance, $10^{-3\cdot2}$ cm. in diameter, a man $10^{2\cdot25}$ cm. high, or Sibbald's Rorqual $10^{1\cdot48}$ metres long. This method, implicit in that of Napier of Merchiston, was first set forth by Wallis, in his *Arithmetica infinitorum*.

of the salt, Ostwald has shewn that we may have particles so minute that they fail to serve as a nucleus for crystallisation—which is as much as to say that they are too small to have the form and properties of a “crystal.” And again, in his thin oil-films, Lord Rayleigh noted the striking change of physical properties which ensues when the film becomes attenuated to one, or something less than one, close-packed layer of molecules, and when, in short, it no longer has the properties of matter *in mass*.

These attenuated films are now known to be “monomolecular,” the long-chain molecules of the fatty acids standing close-packed, like the cells of a honeycomb, and the film being just as thick as the molecules are long. A recent determination makes the several molecules of oleic, palmitic and stearic acids measure 10·4, 14·1 and 15·1 cm. in length, and in breadth 7·4, 6·0 and 5·5 cm., all by 10^{-8} : in good agreement with Lord Rayleigh and Devaux’s lowest estimates (F. J. Hill, *Phil. Mag.* 1929, pp. 940–946). But it has since been shewn that in aliphatic substances the long-chain molecules are not erect, but inclined to the plane of the film; that the zig-zag constitution of the molecules permits them to interlock, so giving the film increased stability; and that the interlock may be by means of a first or second zig-zag, the measured area of the film corresponding precisely to these two dimorphic arrangements. (Cf. C. G. Lyons and E. K. Rideal, *Proc. R.S. (A)*, cxxviii, pp. 468–473, 1930.) The film may be lifted on to a polished surface of metal, or even on a sheet of paper, and one monomolecular layer so added to another; even the complex protein molecule can be unfolded to form a film one amino-acid molecule thick. The whole subject of monomolecular layers, the nature of the film, whether condensed, expanded or gaseous, its astonishing sensitivity to the least impurities, and the manner of spreading of the one liquid over the other, has become of great interest and importance through the work of Irving Langmuir, Devaux, N. K. Adam and others, and throws new light on the whole subject of molecular magnitudes*.

The surface-tension of a drop (as Laplace conceived it) is the cumulative effect, the statistical average, of countless molecular attractions, but we are now entering on dimensions where the molecules are few†. The free surface-energy of a body begins to vary with the *radius*, when that radius is of an order comparable to inter-molecular distances; and the whole expression for such energy tends to vanish away when the radius of the drop or particle is less than $0\cdot01\mu$, or $10m\mu$. The qualities and properties of our

* Cf. (*int. al.*) Adam, *Physics and Chemistry of Surfaces*, 1930; Irving Langmuir, *Proc. R.S. (A)*, clxx, 1939.

† See a very interesting paper by Fred Vles, *Introduction à la physique bactérienne*, *Revue Scient.* 11 juin 1921. Cf. also N. Rashevsky, *Zur Theorie d. spontanen Teilung von mikroskopischen Tropfen*, *Ztschr. f. Physik*, xlvi, p. 578, 1928.

particle suffer an abrupt change here; what then can we attribute, in the way of properties, to a corpuscle or organism as small or smaller than, say, $0\cdot05$ or $0\cdot03\mu$? It must, in all probability, be a homogeneous structureless body, composed of a very small number of albumenoid or other molecules. Its vital properties and functions must be extremely limited; its specific outward characters, even if we could see it, must be *nil*; its osmotic pressure and exchanges must be anomalous, and under molecular bombardment they may be rudely disturbed; its properties can be little more than those of an ion-laden corpuscle, enabling it to perform this or that specific chemical reaction, to effect this or that disturbing influence, or produce this or that pathogenic effect. Had it sensation, its experiences would be strange indeed; for if it could feel, it would regard a fall in temperature as a movement of the molecules around, and if it could see it would be surrounded with light of many shifting colours, like a room filled with rainbows.

The dimensions of a cilium are of such an order that its substance is mostly, if not all, under the peculiar conditions of a surface-layer, and surface-energy is bound to play a leading part in ciliary action. A cilium or flagellum is (as it seems to me) a portion of matter in a state *sui generis*, with properties of its own, just as the film and the jet have theirs. And just as Savart and Plateau have told us about jets and films, so will the physicist some day explain the properties of the cilium and flagellum. It is certain that we shall never understand these remarkable structures so long as we magnify them to another scale, and forget that new and peculiar physical properties are associated with the scale to which they belong*.

As Clerk Maxwell put it, "molecular science sets us face to face with physiological theories. It forbids the physiologist to imagine that structural details of infinitely small dimensions (such as Leibniz assumed, one within another, *ad infinitum*) can furnish an explanation of the infinite variety which exists in the properties and functions of the most minute organisms." And for this reason Maxwell reprobates, with not undue severity, those advocates of pangenesis

* The cilia on the gills of bivalve molluscs are of exceptional size, measuring from say 20 to 120μ long. They are thin triangular plates, rather than filaments; they are from 4 to 10μ broad at the base, but less than 1μ thick. Cf. D. Atkins, *Q.J.M.S.*, 1938, and other papers.

and similar theories of heredity, who "would place a whole world of wonders within a body so small and so devoid of visible structure as a germ." But indeed it scarcely needed Maxwell's criticism to shew forth the immense physical difficulties of Darwin's theory of *pangenesis*: which, after all, is as old as Democritus, and is no other than that Promethean *particula undique desecta* of which we have read, and at which we have smiled, in our Horace.

There are many other ways in which, when we make a long excursion into space, we find our ordinary rules of physical behaviour upset. A very familiar case, analysed by Stokes, is that the viscosity of the surrounding medium has a relatively powerful effect upon bodies below a certain size. A droplet of water, a thousandth of an inch (25μ) in diameter, cannot fall in still air quicker than about an inch and a half per second; as its size decreases, its resistance varies as the radius, not (as with larger bodies) as the surface; and its "critical" or terminal velocity varies as the square of the radius, or as the surface of the drop. A minute drop in a misty cloud may be one-tenth that size, and will fall a hundred times slower, say an inch a minute; and one again a tenth of this diameter (say 0.25μ , or about twice as big as a small micrococcus) will scarcely fall an inch in two hours*. Not only do dust-particles, spores† and bacteria fall, by reason of this principle, very slowly through the air, but all minute bodies meet with great proportionate resistance to their movements through a fluid. In salt water they have the added influence of a larger coefficient of friction than in fresh ‡; and even such comparatively large organisms as the diatoms and the foraminifera, laden though they are with a heavy shell of flint or lime, seem to be poised in the waters of the ocean, and fall with exceeding slowness.

* The resistance depends on the radius of the particle, the viscosity, and the rate of fall (V); the effective weight by which this resistance is to be overcome depends on gravity, on the density of the particle compared with that of the medium, and on the mass, which varies as r^3 . Resistance = $k\pi rV$, and effective weight = $k'r^3$; when these two equal one another we have the critical or terminal velocity, and $V \propto r^2$.

† A. H. R. Buller found the spores of a fungus (*Collybia*), measuring $5 \times 3\mu$, to fall at the rate of half a millimetre per second, or rather more than an inch a minute; *Studies on Fungi*, 1909.

‡ Cf. W. Krause, *Biol. Centralbl.* I, p. 578, 1881; Flügel, *Meteorol. Ztschr.* 1881, p. 321.

When we talk of one thing touching another, there may yet be a distance between, not only measurable but even large compared with the magnitudes we have been considering. Two polished plates of glass or steel resting on one another are still about 4μ apart—the average size of the smallest dust; and when all dust-particles are sedulously excluded, the one plate sinks slowly down to within 0.3μ of the other, an apparent separation to be accounted for by minute irregularities of the polished surfaces*.

The Brownian movement has also to be reckoned with—that remarkable phenomenon studied more than a century ago by Robert Brown†, Humboldt's *facile princeps botanicorum*, and discoverer of the nucleus of the cell‡. It is the chief of those fundamental phenomena which the biologists have contributed, or helped to contribute, to the science of physics.

The quivering motion, accompanied by rotation and even by translation, manifested by the fine granular particle issuing from a crushed pollen-grain, and which Brown proved to have no vital significance but to be manifested by all minute particles whatsoever, was for many years unexplained. Thirty years and more after Brown wrote, it was said to be “due, either directly to some calorical changes continually taking place in the fluid, or to some obscure chemical action between the solid particles and the fluid which is indirectly promoted by heat§.” Soon after these words were

* Cf. Hardy and Nottage, *Proc. R.S. (A)*, cxxviii, p. 209, 1928; Baston and Bowden, *ibid. cxxxiv*, p. 404, 1931.

† *A Brief Description of Microscopical Observations...on the Particles contained in the Pollen of Plants; and on the General Existence of Active Molecules in Organic and Inorganic Bodies*, London, 1828. See also *Edinb. New Philosoph. Journ.* v, p. 358, 1828; *Edinb. Journ. of Science*, i, p. 314, 1829; *Ann. Sc. Nat.* xiv, pp. 341–362, 1828; etc. The Brownian movement was hailed by some as supporting Leibniz's theory of Monads, a theory once so deeply rooted and so widely believed that even under Schwann's cell-theory Johannes Müller and Henle spoke of the cells as “organische Monaden”; cf. Emil du Bois Reymond, *Leibnizische Gedanken in der neueren Naturwissenschaft, Monatsber. d. k. Akad. Wiss., Berlin*, 1870.

‡ The “nucleus” was first seen in the epidermis of Orchids; but “this areola, or nucleus of the cell as perhaps it might be termed, is not confined to the epidermis,” etc. See his paper on Fecundation in Orchideae and Asclepiadace, *Trans. Linn. Soc.* xvi, 1829–33, also *Proc. Linn. Soc.* March 30, 1832.

§ Carpenter, *The Microscope*, edit. 1862, p. 185.

written it was ascribed by Christian Wiener* to molecular movements within the fluid, and was hailed as visible proof of the atomistic (or molecular) constitution of the same. We now know that it is indeed due to the impact or bombardment of molecules upon a body so small that these impacts do not average out, for the moment, to approximate equality on all sides†. The movement becomes manifest with particles of somewhere about 20μ , and is better displayed by those of about 10μ , and especially well by certain colloid suspensions or emulsions whose particles are just below 1μ in diameter‡. The bombardment causes our particles to behave just like molecules of unusual size, and this behaviour is manifested in several ways§. Firstly, we have the quivering movement of the particles; secondly, their movement backwards and forwards, in short, straight disjointed paths; thirdly, the particles rotate, and do so the more rapidly the smaller they are: and by theory, confirmed by observation, it is found that particles of 1μ in diameter rotate on an average through 100° a second, while particles of 13μ turn through only 14° a minute. Lastly, the very curious result appears, that in a layer of fluid the particles are not evenly distributed, nor do they ever fall under the influence of gravity to the bottom. For here gravity and the Brownian movement are rival powers, striving for equilibrium; just as gravity is opposed in the atmosphere by the proper motion of the gaseous molecules. And just as equilibrium is attained in the atmosphere when the molecules are so distributed that the density (and therefore the number of molecules per unit volume) falls off in geometrical

* In *Poggendorff's Annalen*, cxviii, pp. 79–94, 1863. For an account of this remarkable man, see *Naturwissenschaften*, xv, 1927; cf. also Sigmund Exner, Ueber Brown's Molecularbewegung, *Sitzungsber. kk. Akad. Wien*, lvi, p. 116, 1867.

† Perrin, Les preuves de la réalité moléculaire, *Ann. de Physique*, xvii, p. 549, 1905; xix, p. 571, 1906. The actual molecular collisions are unimaginably frequent; we see only the residual fluctuations.

‡ Wiener was struck by the fact that the phenomenon becomes conspicuous just when the size of the particles becomes comparable to that of a wave-length of light.

§ For a full, but still elementary, account, see J. Perrin, *Les Atomes*; cf. also Th. Svedberg, *Die Existenz der Moleküle*, 1912; R. A. Millikan, *The Electron*, 1917, etc. The modern literature of the Brownian movement (by Einstein, Perrin, de Broglie, Smoluchowski and Millikan) is very large, chiefly owing to the value which the phenomenon is shewn to have in determining the size of the atom or the charge on an electron, and of giving, as Ostwald said, experimental proof of the atomic theory.

progression as we ascend to higher and higher layers, so is it with our particles within the narrow limits of the little portion of fluid under our microscope.

It is only in regard to particles of the simplest form that these phenomena have been theoretically investigated*, and we may take it as certain that more complex particles, such as the twisted body of a Spirillum, would shew other and still more complicated manifestations. It is at least clear that, just as the early microscopists in the days before Robert Brown never doubted but that these phenomena were purely vital, so we also may still be apt to confuse, in certain cases, the one phenomenon with the other. We cannot, indeed, without the most careful scrutiny, decide whether the movements of our minutest organisms are intrinsically "vital" (in the sense of being beyond a physical mechanism, or working model) or not. For example, Schaudinn has suggested that the undulating movements of *Spirochaete pallida* must be due to the presence of a minute, unseen, "undulating membrane"; and Doflein says of the same species that "sie verharrt oft mit eigenthümlich zitternden Bewegungen zu einem Orte." Both movements, the trembling or quivering movement described by Doflein, and the undulating or rotating movement described by Schaudinn, are just such as may be easily and naturally interpreted as part and parcel of the Brownian phenomenon.

While the Brownian movement may thus simulate in a deceptive way the active movements of an organism, the reverse statement also to a certain extent holds good. One sometimes lies awake of a summer's morning watching the flies as they dance under the ceiling. It is a very remarkable dance. The dancers do not whirl or gyrate, either in company or alone; but they advance and retire; they seem to jostle and rebound; between the rebounds they dart hither or thither in short straight snatches of hurried flight, and turn again sharply in a new rebound at the end of each little rush†.

* Cf. R. Gans, *Wie fallen Stäbe und Scheiben in einer reibenden Flüssigkeit?* *Münchener Bericht*, 1911, p. 191; K. Przibram, *Ueber die Brown'sche Bewegung nicht kugelförmiger Teilchen*, *Wiener Bericht*, 1912, p. 2339; 1913, pp. 1895-1912.

† As Clerk Maxwell put it to the British Association at Bradford in 1873, "We cannot do better than observe a swarm of bees, where every individual bee is flying furiously, first in one direction and then in another, while the swarm as a whole is either at rest or sails slowly through the air."

Their motions are erratic, independent of one another, and devoid of common purpose*. This is nothing else than a vastly magnified picture, or simulacrum, of the Brownian movement; the parallel between the two cases lies in their complete irregularity, but this in itself implies a close resemblance. One might see the same thing in a crowded market-place, always provided that the bustling crowd had no business whatsoever. In like manner Lucretius, and Epicurus before him, watched the dust-motes quivering in the beam, and saw in them a mimic representation, *rei simulacrum et imago*, of the eternal motions of the atoms. Again the same phenomenon may be witnessed under the microscope, in a drop of water swarming with Paramoecia or such-like Infusoria; and here the analogy has been put to a numerical test. Following with a pencil the track of each little swimmer, and dotting its place every few seconds (to the beat of a metronome), Karl Przibram found that the mean successive distances from a common base-line obeyed with great exactitude the "Einstein formula," that is to say the particular form of the "law of chance" which is applicable to the case of the Brownian movement†. The phenomenon is (of course) merely analogous, and by no means identical with the Brownian movement; for the range of motion of the little active organisms, whether they be gnats or infusoria, is vastly greater than that of the minute particles which are passive under bombardment; nevertheless Przibram is inclined to think that even his comparatively large infusoria are small enough for the molecular bombardment to be a stimulus, even though not the actual cause, of their irregular and interrupted movements‡.

* Nevertheless there may be a certain amount of bias or direction in these seemingly random divagations: cf. J. Brownlee, *Proc. R.S.E.* xxxi, p. 262, 1910-11; F. H. Edgeworth, *Metron*, i, p. 75, 1920; Lotka, *Elem. of Physical Biology*, 1925, p. 344.

† That is to say, the mean square of the displacements of a particle, in any direction, is proportional to the interval of time. Cf. K. Przibram, Ueber die ungeordnete Bewegung niederer Tiere, *Pflüger's Archiv*, CLIII, pp. 401-405, 1913; *Arch. f. Entw. Mech.* XLII, pp. 20-27, 1917.

‡ All that is actually proven is that "pure chance" has governed the movements of the little organism. Przibram has made the analogous observation that infusoria, when not too crowded together, spread or diffuse through an aperture from one vessel to another at a rate very closely comparable to the ordinary laws of molecular diffusion.

George Johnstone Stoney, the remarkable man to whom we owe the name and concept of the *electron*, went further than this; for he supposed that molecular bombardment might be the source of the life-energy of the bacteria. He conceived the swifter moving molecules to dive deep into the minute body of the organism, and this in turn to be able to make use of these importations of energy*.

We draw near the end of this discussion. We found, to begin with, that "scale" had a marked effect on physical phenomena, and that increase or diminution of magnitude might mean a complete change of statical or dynamical equilibrium. In the end we begin to see that there are discontinuities in the scale, defining phases in which different forces predominate and different conditions prevail. Life has a range of magnitude narrow indeed compared to that with which physical science deals; but it is wide enough to include three such discrepant conditions as those in which a man, an insect and a bacillus have their being and play their several roles. Man is ruled by gravitation, and rests on mother earth. A water-beetle finds the surface of a pool a matter of life and death, a perilous entanglement or an indispensable support. In a third world, where the bacillus lives, gravitation is forgotten, and the viscosity of the liquid, the resistance defined by Stokes's law, the molecular shocks of the Brownian movement, doubtless also the electric charges of the ionised medium, make up the physical environment and have their potent and immediate influence on the organism. The predominant factors are no longer those of our scale; we have come to the edge of a world of which we have no experience, and where all our preconceptions must be recast.

* *Phil. Mag.* April 1890.

CHAPTER III

THE RATE OF GROWTH

WHEN we study magnitude by itself, apart from the gradual changes to which it may be subject, we are dealing with a something which may be adequately represented by a number, or by means of a line of definite length; it is what mathematicians call a scalar phenomenon. When we introduce the conception of change of magnitude, of magnitude which varies as we pass from one point to another in space, or from one instant to another in time, our phenomenon becomes capable of representation by means of a line of which we define both the length and the direction; it is (in this particular aspect) what is called a vector phenomenon.

When we deal with magnitude in relation to the dimensions of space, our diagram plots magnitude in one direction against magnitude in another—length against height, for instance, or against breadth; and the result is what we call a picture or outline, or (more correctly) a “plane projection” of the object. In other words, what we call Form is a ratio of magnitudes* referred to direction in space.

When, in dealing with magnitude, we refer its variations to successive intervals of time (or when, as it is said, we equate it with time), we are then dealing with the phenomenon of growth; and it is evident that this term growth has wide meanings. For growth may be positive or negative, a thing may grow larger or smaller, greater or less; and by extension of the concrete signification of the word we easily and legitimately apply it to non-material things, such as temperature, and say, for instance, that a body “grows” hot or cold. When in a two-dimensional diagram we represent a magnitude (for instance length) in relation to time (or “plot” length against time, as the phrase is), we get that kind of vector diagram which is known as a “curve of growth.” We see that the phenomenon which we are studying is a *velocity* (whose “dimensions” are space/time, or L/T), and this phenomenon we shall speak of, simply, as a *rate of growth*.

In various conventional ways we convert a two-dimensional into

* In Aristotelian logic, Form is a *quality*. None the less, it is related to *quantity*; and we find the Schoolmen speaking of it as *qualitas circa quantitatem*.

a three-dimensional diagram. We do so, for example, when, by means of the geometrical method of "perspective," we represent upon a sheet of paper the length, breadth and depth of an object in three-dimensional space, but we do it better by means of contour-lines or "isopleths." By contour-lines superposed upon a map of a country, we shew its hills and valleys; and by contour-lines we may shew temperature, rainfall, population, language, or any other "third dimension" related to the two dimensions of the map. *Time* is always implicit, in so far as each map refers to its own date or epoch; but Time as a dimension can only be substituted for one of the three dimensions already there. Thus we may superpose upon our map the successive outlines of the coast from remote antiquity, or of any single isotherm or isobar from day to day. And if in like manner we superpose on one another, or even set side by side, the outlines of a growing organism—for instance of a young leaf and an old, we have a three-dimensional diagram which is a partial representation (limited to two dimensions of *space*) of the organism's gradual change of form, or course of development; in such a case our contours may, for the purposes of the embryologist, be separated by time-intervals of a few hours or days, or, for the palaeontologist, by interspaces of unnumbered and innumerable years*.

Such a diagram represents in two of its three dimensions form, and in two (or three) of its dimensions growth, and we see how intimately the two concepts are correlated or interrelated to one another. In short it is obvious that the *form* of an organism is determined by its rate of *growth* in various directions; hence rate of growth deserves to be studied as a necessary preliminary to the theoretical study of form, and organic form itself is found, mathematically speaking, to be a *function of time*†.

* Sometimes we find one and the same diagram suffice, whether the time-intervals be great or small; and we then invoke "Wolff's law" (or Kielmeyer's), and assert that the life-history of the individual repeats, or recapitulates, the history of the race. This "recapitulation theory" was all-important in nineteenth-century embryology, but was criticised by Adam Sedgwick (*Q.J.M.S.* xxxvi, p. 38, 1894) and many later authors; cf. J. Needham, *Chemical Embryology*, 1931, pp. 1629–1647.

† Our subject is one of Bacon's "Instances of the Course" or studies wherein we "measure Nature by periods of Time." In Bacon's *Catalogue of Particular Histories*, one of the odd hundred histories or investigations which he foreshadows is precisely that which we are engaged on, viz. a "History of the Growth and Increase of the Body, in the whole and in its parts."

At the same time, we need only consider this large part of our subject somewhat briefly. Though it has an essential bearing on the problems of morphology, it is in greater degree involved with physiological problems; also, the statistical or numerical aspect of the question is peculiarly adapted to the mathematical study of variation and correlation. These important subjects we must not neglect; but our main purpose will be served if we consider the characteristics of a rate of growth in a few illustrative cases, and recognise that this rate of growth is a very important specific property, with its own characteristic value in this organism or that, in this or that part of each organism, and in this or that phase of its existence.

The statement which we have just made that "the form of an organism is determined by its rate of growth in various directions," is one which calls for further explanation and for some measure of qualification.

Among organic forms we shall have many an occasion to see that form may be due in simple cases to the direct action of certain molecular forces, among which surface-tension plays a leading part. Now when surface-tension causes (for instance) a minute semifluid organism to assume a spherical form, or gives to a film of protoplasm the form of a catenary or of an elastic curve, or when it acts in various other ways productive of definite contours—just as it does in the making of a drop, a splash or a jet—this is a process of conformation very different from that by which an ordinary plant or animal grows into its specific form. In both cases change of form is brought about by the movement of portions of matter, and in both cases it is ultimately due to the action of molecular forces; but in the one case the movements of the particles of matter lie for the most part within molecular range, while in the other we have to deal with the transference of portions of matter into the system from without, and from one widely distant part of the organism to another. It is to this latter class of phenomena that we usually restrict the term growth; it is in regard to them that we are in a position to study the *rate of action* in different directions and at different times, and to realise that it is on such differences of rate that form and its modifications essentially and ultimately depend.

The difference between the two classes of phenomena is akin to the difference between the forces which determine the form of a raindrop and those which, by the flowing of the waters and the sculpturing of the solid earth, have brought about the configuration of a river or a hill; *molecular* forces are paramount in the one, and *molar* forces are dominant in the other.

At the same time, it is true that *all* changes of form, inasmuch as they necessarily involve changes of actual and relative magnitude, may in a sense be looked upon as phenomena of growth; and it is also true, since the movement of matter must always involve an element of time*, that in all cases the *rate of growth* is a phenomenon to be considered. Even though the molecular forces which play their part in modifying the form of an organism exert an action which is, theoretically, all but instantaneous, that action is apt to be dragged out to an appreciable interval of time by reason of viscosity or some other form of resistance in the material. From the physical or physiological point of view the rate of action may be well worth studying even in such cases as these; for example, a study of the rate of cell-division in a segmenting egg may teach us something about the work done, and the various energies concerned. But in such cases the action is, as a rule, so homogeneous, and the form finally attained is so definite and so little dependent on the time taken to effect it, that the specific rate of change, or rate of growth, does not enter into the morphological problem.

We are dealing with Form in a very concrete way. To Aristotle it was a metaphysical concept; to us it is a quasi-mechanical effect on Matter of the operation of chemico-physical forces†. To

* Cf. Aristotle, *Phys.* vi, 5, 235a, 11, ἐπεὶ γὰρ ἄπασα κίνησις ἐν χρόνῳ, κτλ.; he had already told us that natural science deals with magnitude, with motion and with time: ἔστιν η̄ περὶ φύσεως ἐπιστήμη περὶ μέγεθος καὶ κίνησιν καὶ χρόνου. Hence *omnis velocitas tempore durat* became a scholastic aphorism. Bacon emphasised, in like manner, the fact that "all motion or natural action is performed in time: some more quickly, some more slowly, but all in periods determined and fixed in the nature of things. Even those actions which seem to be performed suddenly, and (as we say) in the twinkling of an eye, are found to admit of degree in respect of duration" (*Nov. Organon*, XLVI). That infinitely small motions take place in infinitely small intervals of time is the concept which lies at the root of the calculus. But there is another side to the story.

† Cf. N. K. Koltzoff, Physikalisch-chemische Grundlage der Morphologie, *Biol. Centralbl.* 1928, pp. 345-369.

Aristotle its Form was the essence, the archetype, the very "nature" of a thing, and Matter and Form were an inseparable duality. Even now, when we divide our science into Physiology and Morphology, we are harking back to the old Aristotelian antithesis.

To sum up, we may lay down the following general statements. The form of organisms is a phenomenon to be referred in part to the direct action of molecular forces, in larger part to a more complex and slower process, indirectly resulting from chemical, osmotic and other forces, by which material is introduced into the organism and transferred from one part of it to another. It is this latter complex phenomenon which we usually speak of as "growth."

Every growing organism, and every part of such a growing organism, has its own specific rate of growth, referred to this or that particular direction; and it is by the ratio between these rates in different directions that we must account for the external forms of all save certain very minute organisms. This ratio may sometimes be of a *simple* kind, as when it results in the mathematically definable outline of a shell, or the smooth curve of the margin of a leaf. It may sometimes be a very *constant* ratio, in which case the organism while growing in bulk suffers little or no perceptible change in form; but such constancy seldom endures beyond a season, and when the ratios tend to alter, then we have the phenomenon of morphological "*development*," or steady and persistent alteration of form.

This elementary concept of Form, as determined by varying rates of Growth, was clearly apprehended by the mathematical mind of Haller—who had learned his mathematics of the great John Bernoulli, as the latter in turn had learned his physiology from the writings of Borelli*. It was this very point, the apparently unlimited extent to which, in the development of the chick, inequalities of growth could and did produce changes of form and changes of anatomical structure, that led Haller to surmise that the process was actually without limits, and that all development was but an unfolding or "*evolutio*," in which no part came into being which

* "Qua in re Incomparabilis Viri Joh. Alph. Borelli vestigiis insistemus." Joh. Bernoulli, *De motu muscularorum*, 1694.

had not essentially existed before*. In short the celebrated doctrine of "preformation" implied on the one hand a clear recognition of what growth can do throughout the several stages of development, by hastening the increase in size of one part, hindering that of another, changing their relative magnitudes and positions, and so altering their forms; while on the other hand it betrayed a failure (inevitable in those days) to recognise the essential difference between these movements of masses and the molecular processes which precede and accompany them, and which are characteristic of another order of magnitude.

The general connection between growth and form has been recognised by other writers besides Haller. Such a connection is implicit in the "proportional diagrams" by which Dürer and his brother-artists illustrated the changes in form, or of relative dimensions, which mark the child's growth to boyhood and to manhood. The same connection was recognised by the early embryologists, and appears, as a survival of the doctrine of preformation, in Pander's† study of the development of the chick. And long afterwards, the embryological aspect of the case was emphasised by His‡, who pointed out that the foldings of the blastoderm, by which the neural and amniotic folds are brought into being, were the resultant of unequal rates of growth in what to begin with was a uniform layer of embryonic tissue. If a sheet of paper be made to expand here and contract there, as by moisture or evaporation, the plane surface becomes dimpled, or folded, or buckled, by the said expansions and contractions; and the distortions to which the surface of the "germinal disc" is subject are, as His shewed once and for all, precisely analogous. There are

* Cf. (e.g.) *Elem. Physiologiae*, ed. 1766, VIII, p. 114, "Ducimur autem ad evolutionem potissimum, quando a perfecto animale retrorsum progradimur, et incrementorum atque mutationum seriem relegimus. Ita inveniemus perfectum illud animal fuisse imperfectius, alterius figurae et fabricae, et denique rude et informe: et tamen idem semper animal sub iis diversis phasibus fuisse, quae absque ullo saltu perpetuos parvosque per gradus cohaereant."

† *Beiträge zur Entwicklungsgeschichte des Hühnchens im Ei*, 1817, p. 40. Roux ascribes the same views also to Von Baer and to R. H. Lotze (*Allgem. Physiologie*, 1851, p. 353).

‡ W. His, *Unsere Körperform, und das physiologische Problem ihrer Entstehung*, 1874. See also *Archiv f. Anatomie*, 1894; and cf. C. B. Davenport, Processes concerned in Ontogeny, *Bull. Mus. Comp. Anat.* xxvii, 1895; also G. Dehnel and Jan Tur, *De Embryonum evolutionis progressu inequali: Kosmos* (Lwow), LIII, 1928.

certain Nostoc-algae in which unequal growth, ceasing towards the periphery of a disc and increasing here and there within, gives rise to folds and bucklings curiously like those of our own ears: which indeed owe their shape and characteristic folding to an identical or analogous cause.

An experimental demonstration comparable to the actual case is obtained by making an "artificial blastoderm" of little pills or pellets of dough, which are caused to grow at varying rates by the addition of varying quantities of yeast. Here, as Roux is careful to point out,* it is not only the *growth* of the individual cells, but the *traction* exercised on one another through their mutual interconnections, which brings about foldings, wrinkleings and other distortions of the structure. But this again, or such as this, had been in Haller's mind, and formed an essential part of his embryological doctrine. For he has no sooner treated of *incrementum*, or *celeritas incrementi*, than he proceeds to deal with the contributory and complementary phenomena of expansion, traction (*adtractio*)† and pressure, and the more subtle influences which he denominates *vis derivationis et revulsionis*‡: these latter being the secondary and correlated effects on growth in one part, brought about by such changes as are produced, for instance in the circulation, by the growth of another.

We have to do with growth, with exquisitely graded or balanced growth, and with forces subtly exerted by one growing part upon another, in so wonderful a piece of work as the development of the eye: as its primary vesicle expands and then dimples in, as the lens appears and fits into place, as the secondary vesicle closes over to form iris and pupil, and in all the rest of the story.

Let us admit that, on the physiological side, Haller's or His's methods of explanation carry us but a little way; yet even this little way is something gained. Nevertheless, I can well remember

* Roux, *Die Entwickelungsmechanik*, 1905, p. 99.

† *Op. cit.* p. 302, "Magnum hoc naturae instrumentum, etiam in corpore animato evolvendo potenter operatur, etc." The recurrent laryngeal nerve, drawn down as its arch of the aorta descends, is a simple instance of anatomical *traction*. The vitelline and omphalomesenteric arteries lead, by more complicated constraints and tractions, to the characteristic loops of the intestinal blood-vessels, and of the intestine itself. Cf. G. Enbom, *Lunds Univ. Arsskrift*, 1939.

‡ *Ibid.* p. 306, "Subtiliora ista, et aliquantum hypothesi mista, tamen magnam mihi videntur speciem veri habere."

the harsh criticism and even contempt which His's doctrine met with, not merely on the ground that it was inadequate, but because such an explanation was deemed wholly inappropriate, and was utterly disavowed*. Oscar Hertwig, for instance, asserted that, in embryology, when we find one embryonic stage preceding another, the existence of the former is, for the embryologist, an all-sufficient "causal explanation" of the latter. "We consider (he says) that we are studying and explaining a causal relation when we have demonstrated that the gastrula arises by invagination of a blastosphere, or the neural canal by the infolding of a cell-plate so as to constitute a tube†." For Hertwig, then, as Roux remarks, the task of investigating a physical mechanism in embryology—"der Ziel das Wirken zu erforschen"—has no existence at all. For Balfour also, as for Hertwig, the mechanical or physical aspect of organic development had little or no attraction. In one notable instance, Balfour himself adduced a physical, or quasi-physical, explanation of an organic process, when he referred the various modes of segmentation of an ovum, complete or partial, equal or unequal and so forth, to the varying amount or varying distribution of food-yolk associated with the germinal protoplasm of the egg. But in the main, like all the other embryologists of his day, Balfour was engrossed in the

* Cf. His, On the Principles of Animal Morphology, *Proc. R.S.E.* xv, p. 294, 1888: "My own attempts to introduce some elementary mechanical or physiological conceptions into embryology have not generally been agreed to by morphologists. To one it seemed ridiculous to speak of the elasticity of the germinal layers; another thought that, by such considerations, we 'put the cart before the horse'; and one more recent author states, that we have better things to do in embryology than to discuss tensions of germinal layers and similar questions, since all explanations must of necessity be of a phylogenetic nature. This opposition to the application of the fundamental principles of science to embryological questions would scarcely be intelligible had it not a dogmatic background. No other explanation of living forms is allowed than heredity, and any which is founded on another basis must be rejected.... To think that heredity will build organic beings without mechanical means is a piece of unscientific mysticism." Even the school of *Entwickelungsmechanik* showed a certain reluctance, or extreme caution, in speaking of the *physical* forces in relation to embryology or physiology. This reluctant caution is well exemplified by Martin Heidenhain, writing on "Formen und Kräfte in der lebendigen Natur" in Roux's *Vorträge*, xxxii, 1923. Speaking of "die Kräfte welche die Entwicklung und den fertigen Zustand der Formen bedingen", he says: "letztere kann man aber nicht auf dem Felde der Physik suchen, sondern nur im Umkreis der Lebendigen, obwohl anzunehmen ist, dass diese Kräfte später einmal 'analogienhaft' nach dem Vorbilde der Physik beschreibbar sein werden"

† O. Hertwig, *Zeit- und Streiffragen der Biologie*, II, 1897.

problems of phylogeny, and he expressly defined the aims of comparative embryology (as exemplified in his own textbook) as being "twofold: (1) to form a basis for Phylogeny, and (2) to form a basis for Organogeny, or the origin and evolution of organs*."

It has been the great service of Roux and his fellow-workers of the school of "Entwickelungsmechanik," and of many other students to whose work we shall refer, to try, as His tried, to import into embryology, wherever possible, the simpler concepts of physics, to introduce along with them the method of experiment, and to refuse to be bound by the narrow limitations which such teaching as that of Hertwig would of necessity impose on the work and the thought and the whole philosophy of the biologist.

Before we pass from this general discussion to study some of the particular phenomena of growth, let me give an illustration, from Darwin, of a point of view which is in marked contrast to Haller's simple but essentially mathematical conception of Form.

There is a curious passage in the *Origin of Species*†, where Darwin is discussing the leading facts of embryology, and in particular Von Baer's "law of embryonic resemblance." Here Darwin says: "We are so much accustomed to see a difference in structure between the embryo and the adult that we are tempted to look at this difference as in some necessary manner contingent on growth. But there is no reason why, for instance, the wing of a bat, or the fin of a porpoise, should not have been sketched out with all their parts in proper proportion, as soon as any part became visible." After pointing out various exceptions, with his habitual care, Darwin proceeds to lay down two general principles, viz. "that slight variations generally appear at a not very early period of life," and secondly, that "at whatever age a variation first appears in the parent, it tends to reappear at a corresponding age in the offspring." He then argues that it is with nature as with the fancier, who does not care what his pigeons look like in the embryo so long as the full-grown bird possesses the desired qualities: and that the process of selection takes place when the birds or other animals are nearly

* *Treatise on Comparative Embryology*, I, p. 4, 1881.

† 1st ed. p. 444; 6th ed. p. 390. The student should not fail to consult the passage in question; for there is always a risk of misunderstanding or misinterpretation when one attempts to epitomise Darwin's carefully condensed arguments.

grown up—at least on the part of the breeder, and presumably in nature as a general rule. The illustration of these principles is set forth as follows: “Let us take a group of birds, descended from some ancient form and modified through natural selection for different habits. Then, from the many successive variations having supervened in the several species at a not very early age, and having been inherited at a corresponding age, the young will still resemble each other much more closely than do the adults—just as we have seen with the breeds of the pigeon.... Whatever influence long-continued use or disuse may have had in modifying the limbs or other parts of any species, this will chiefly or solely have affected it when nearly mature, when it was compelled to use its full powers to gain its own living; and the effects thus produced will have been transmitted to the offspring at a corresponding nearly mature age. Thus the young will not be modified, or will be modified only in a slight degree, through the effects of the increased use or disuse of parts.” This whole argument is remarkable, in more ways than we need try to deal with here; but it is especially remarkable that Darwin should begin by casting doubt upon the broad fact that a “difference in structure between the embryo and the adult” is “in some necessary matter contingent on growth”; and that he should see no reason why complicated structures of the adult “should not have been sketched out with all their parts in proper proportion, as soon as any part became visible.” It would seem to me that even the most elementary attention to form in its relation to growth would have removed most of Darwin’s difficulties in regard to the particular phenomena which he is considering here. For these phenomena are phenomena of form, and therefore of relative magnitude; and the magnitudes in question are attained by growth, proceeding with certain specific velocities, and lasting for certain long periods of time. And it seems obvious accordingly that in any two related individuals (whether specifically identical or not) the differences between them must manifest themselves gradually, and be but little apparent in the young. It is for the same simple reason that animals which are of very different sizes when adult differ less and less in size (as well as form) as we trace them backwards to their early stages.

Though we study the visible effects of varying rates of growth

throughout wellnigh all the problems of morphology, it is not very often that we can directly measure the velocities concerned. But owing to the obvious importance of the phenomenon to the morphologist we must make shift to study it where we can, even though our illustrative cases may seem sometimes to have little bearing on the morphological problem*.

In a simple spherical organism, such as the single spherical cell of *Protococcus* or of *Orbulina*, growth is reduced to its simplest terms, and indeed becomes so simple in its outward manifestations that it loses interest to the morphologist. The rate of growth is measured by the rate of change in length of a radius, i.e. $V = (R' - R)/T$, and from this we may calculate, as already indicated, the rate in terms of surface and of volume. The growing body remains of constant form, by the symmetry of the system; because, that is to say, on the one hand the pressure exerted by the growing protoplasm is exerted equally in all directions, after the manner of a hydrostatic pressure, which indeed it actually is; while on the other hand the "skin" or surface layer of the cell is sufficiently homogeneous to exert an approximately uniform resistance. Under these simple conditions, then, the rate of growth is uniform in all directions, and does not affect the form of the organism.

But in a larger or a more complex organism the study of growth, and of the rate of growth, presents us with a variety of problems, and the whole phenomenon (apart from its physiological interest) becomes a factor of great morphological importance. We no longer find that growth tends to be uniform in all directions, nor have we any reason to expect it should. The resistances which it meets with are no longer uniform. In one direction but not in others it will be opposed by the important resistance of gravity; within the growing system itself all manner of structural differences come into play, and set up unequal resistances to growth in one direction or another. At the same time the actual sources of growth, the chemical and osmotic forces which lead to the intussusception of new matter, are not uniformly distributed; one tissue or one organ may well increase while another does not; a set of bones, their intervening cartilages and their surrounding muscles, may all be

* "In omni rerum naturalium historia utile est mensuras definiri et numeros," Haller, *Elem. Physiol.* II, p. 258, 1760. Cf. Hales, *Vegetable Staticks*, Introduction.

capable of very different rates of increment. The changes of form which result from these differences in rate are especially manifested during that phase of life when growth itself is rapid: when the organism, as we say, is undergoing its *development*.

When growth in general has slowed down, the differences in rate between different parts of the organism may still exist, and may be made manifest by careful observation and measurement, but the resultant change of form is less apt to strike the eye. Great as are the differences between the rates of growth in different parts of a complex organism, the marvel is that the ratios between them are so nicely balanced as they are, and so capable of keeping the form of the growing organism all but unchanged for long periods of time, or of slowly changing it in its own harmonious way. There is the nicest possible balance of forces and resistances in every part of the complex body; and when this normal equilibrium is disturbed, then we get abnormal growth, in the shape of tumours and exostoses, and other malformations and deformities of every kind.

The rate of growth in man

Man will serve us as well as another organism for our first illustrations of rate of growth, nor can we easily find another which we can better study from birth to the utmost limits of old age. Nor can we do better than go for our first data concerning him to Quetelet's *Essai de Physique Sociale*, an epoch-making book for the biologist. For it is packed with information, some of it unsurpassed, in regard to human growth and form; and it stands out as the first great essay in which social statistics and organic variation are dealt with from the point of view of the mathematical theory of probabilities. How on the one hand Quetelet followed Da Vinci, Luca Pacioli and Dürer in studying the growth and proportions of man: and how on the other he simplified and extended the ideas of James Bernoulli, of d'Alembert, Laplace, Poisson and the rest, is another and a vastly interesting story*.

* Quetelet, *Sur l'Homme*. . . , ou *Essai de Physique Sociale*, Bruxelles, 1835: trans. Edinburgh, 1842; also *Instructions populaires sur le calcul des probabilités*, 1828; *Lettres . . . sur la théorie des probabilités appliquée aux sciences morales et politiques*, 1846; and *Anthropométrie*, 1871. For an account of his life and writings, see Lottin's *Quetelet, statisticien et sociologue*, Louvain, 1912; also J. M. Keynes. *Treatise on Probability*, 1921.

The meaning of the word "statistics" is curiously changed. For Shakespeare or for Milton a statist meant (so Dr Johnson says) "a politician, a statesman; one skilled in government." The eighteenth-century *Statistical Account of Scotland* was a description of the State and of its people, its wealth, its agriculture and its trade.

Stature and weight of man (from Quetelet's Belgian data,
Essai, II, pp. 23-43; Anthropométrie, p. 346)†*

Age	Stature in metres			Weight in kgm.			$W/L^3 \times 100$	
	Male	Female	% F/M	Male	Female	% F/M	Male	Female
0	0.50	0.48	96.0	3.20	2.91	90.9	2.56	2.64
1	0.70	0.69	98.6	10.00	9.30	93.0	2.92	2.83
2	0.80	0.78	97.5	12.00	11.40	95.0	2.35	2.40
3	0.86	0.85	98.8	13.21	12.45	94.2	2.09	2.03
4	0.93	0.91	97.6	15.07	14.18	94.1	1.84	1.88
5	0.99	0.97	98.4	16.70	15.50	92.8	1.89	1.69
6	1.05	1.03	98.6	18.04	16.74	92.8	1.56	1.53
7	1.11	1.10	98.6	20.16	18.45	91.5	1.48	1.39
8	1.17	1.14	97.3	22.26	19.82	89.0	1.39	1.34
9	1.23	1.20	97.8	24.09	22.44	93.2	1.29	1.30
10	1.28	1.25	97.3	26.12	24.24	92.8	1.25	1.24
11	1.33	1.28	96.1	27.85	26.25	94.3	1.18	1.25
12	1.36	1.33	97.6	31.00	30.54	98.5	1.23	1.38
13	1.40	1.39	98.8	35.32	34.65	98.1	1.29	1.29
14	1.49	1.45	97.3	40.50	38.10	94.1	1.21	1.25
15	1.56	1.47	94.6	46.41	41.30	89.0	1.22	1.30
16	1.61	1.52	93.2	53.39	44.44	83.2	1.20	1.32
17	1.67	1.54	92.5	57.40	49.08	85.5	1.23	1.34
18	1.70	1.56	91.9	61.26	53.10	86.7	1.24	1.40
19	1.71	—	—	63.32	—	—	1.20	—
20	1.71	1.57	91.8	65.00	54.46	83.8	1.30	1.41
25	1.72	1.58	91.6	68.29	55.08	80.7	1.39	1.39
30	1.72	1.58	91.7	68.90	55.14	80.0	1.35	1.39
40	1.71	1.56	90.8	68.81	56.65	82.3	1.38	1.49
50	1.67	1.54	91.8	67.45	58.45	86.7	1.45	1.59
60	1.64	1.52	92.5	65.50	56.73	86.6	1.48	1.61
70	1.62	1.51	93.3	63.03	53.72	85.2	1.48	1.58
80	1.61	1.51	93.4	61.22	51.52	84.1	1.46	1.50

This is what Sir William Petty had meant in the seventeenth century by his *Political Arithmetic*, and what Quetelet meant in the nineteenth by his *Physique Sociale*. But "statistics" nowadays are counts and measures of all sorts of things; and statistical science arranges,

* The figures for height and weight given in my first edition were Quetelet's smoothed or adjusted values. I have gone back to his original data.

† This "almost steady growth," from about seven years old to eleven, means that the curve of growth is a nearly straight line during this period: a result already found by Elderton for Glasgow children (*Biometrika*, x, p. 293, 1914-15), by Fessard and Laufer in Paris (*Nouvelles Tables de Croissance*, 1935, p. 13), etc.

explains, and draws deductions from, the resulting series and arrays of numbers. It deals with simple and measurable effects, due to complex and often unknown causes; and when experiment is not at hand to disentangle these causes, statistical methods may still do something to elucidate them.

Now as to the growth of man, if the child be some 20 inches, or say 50 cm., tall at birth, and the man some six feet, or 180 cm., high at twenty, we may say that his average rate of growth had

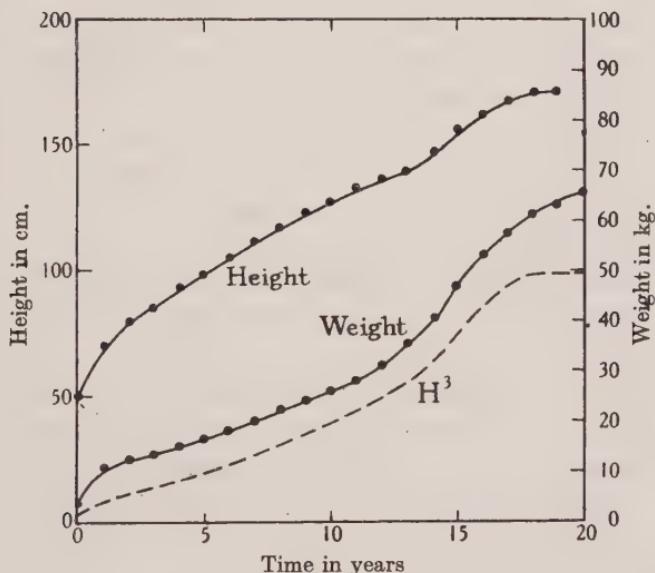


Fig. 4. Curve of growth in man. From Quetelet's Belgian data.
The curve H^3 is proportional to the height cubed.

been $(180 - 50)/20$ cm., or 6.5 cm. per annum. But we well know that this is but a rough preliminary statement, and that growth was surely quick during some and slow during other of those twenty years; we must learn not only the result of growth but the course of growth; we must study it in its *continuity*. This we do, in the first instance, by the method of coordinates, plotting magnitude against time. We measure time along a certain axis (x), and the magnitude in question along a coordinate axis (y); a succession of points defines the magnitudes reached at corresponding epochs, and these points constitute a "curve of growth" when we join them together.

Our curve of growth, whether for weight or stature, has a definite form or characteristic curvature: this being a sign that the rate of growth is not always the same but changes as time goes on. Such as it is, the curvature alters in an orderly way; so that, apart from minor and "fortuitous" irregularities, our curves of growth tend to be smooth curves. And the fact that they are so is an instance of that "principle of continuity" which is the foundation of all physical and natural science.

The curve of growth (Fig. 4) for length or stature in man indicates a rapid increase at the outset, during the quick growth of babyhood; a long period of slower but almost steady growth in boyhood; as a rule a marked quickening in his early teens, when the boy comes to the "growing age"; and a gradual arrest of growth as he "comes to his full height" and reaches manhood. If we carried the curve farther, we should see a very curious thing. We should see that a man's full stature endures but for a spell; long before fifty* it has begun to abate, by sixty it is notably lessened, in extreme old age the old man's frame is shrunken and it is but a memory that "he once was tall"; the decline sets in sooner in women than in men, and "a little old woman" is a household word. We have seen, and we see again, that growth may have a negative value, pointing towards an inevitable end. The phenomenon of negative growth extends to weight also; it is largely chemical in origin; the metabolism of the body is impaired, and the tissues keep pace no longer with senile wastage and decay.

We must be very careful, however, how we interpret such a Table as this; for it records the character of a *population*, and we are apt to read in it the life-history of the *individual*. The two things are not necessarily the same. That a man grows less as he grows older all old men know; but it may also be the case, and our Table may indicate it, that the short men live longer than the tall.

Our curve of growth is, by implication, a "time-energy" diagram † or diagram of activity. As man grows he is absorbing energy beyond his daily needs, and accumulating it at a rate depicted in

* Dr Johnson was not far wrong in saying that "life declines from thirty-five"; though the Autoocrat of the Breakfast-table declares, like Cicero, that "the furnace is in full blast for ten years longer".

† J. Joly, *The Abundance of Life*, 1915 (1890), p. 86.

our curve; till the time comes when he accumulates no longer, and is constrained to draw upon his dwindling store. But in part, the slow decline in stature is a sign of the unequal contest between our bodily powers and the unchanging force of gravity, which draws us down when we would fain rise up*; we strive against it all our days, in every movement of our limbs, in every beat of our hearts. Gravity makes a difference to a man's height, and no slight one, between the morning and the evening; it leaves its mark in sagging wrinkles, drooping mouth and hanging breasts; it is the indomitable force which defeats us in the end, which lays us on our death-bed and lowers us to the grave†. But the grip in which it holds us is the title by which we live; were it not for gravity one man might hurl another by a puff of his breath into the depths of space, beyond recall for all eternity‡.

Side by side with the curve which represents growth in length, or height or stature, our diagram shews the corresponding curve of weight. That this curve is of a different shape from the former one is accounted for in the main (though not wholly) by the fact—which we have already dealt with—that in similar bodies volume, and therefore weight, varies as the cubes of the linear dimensions; and drawing a third curve to represent the cubes of the corresponding heights, it now resembles the curve of weight pretty closely, but still they are not quite the same. There is a change of direction, or “point of inflection,” in the curve of weight at one or two years old, and there are certain other features in our curves which the scale of the diagram does not make clear; and all these differences are due to the fact that the child is changing shape as he grows, that other linear dimensions grow somewhat differently from

* “Lou pes, mèstre de tout (Le poids, maître de tout), mèstre sènso vergougnو, Que te tirasso en bas de sa brutalo pougno.” J. H. Fabre, *Oubreto prouvençalo*, p. 61.

† The continuity of the phenomenon of growth, and the natural passage from the phase of increase to that of decrease or decay, are admirably discussed by Enriques, in *La Morte*, *Rivista di Scienza*, 1907, and in *Wachstum und seine analytische Darstellung*, *Biol. Centralbl.* June, 1909. Haller (*Elementa*, vii, p. 68) recognised *decrementum* as a phase of growth, not less important (theoretically) than *incrementum*; “*tristis, sed copiosa, haec est materies.*”

‡ Boscovich, *Theoria*, para. 552, “*Homo hominem arreptum a Tellure, et utecumque exigua impulsu vi vel uno etiam oris flatu impeditum, ab hominum omnium commercio in infinitum expelleret, nunquam per totam aeternitatem redditurum.*”

Annual increment of stature (in cm.) from Belgian, French and American statistics

Age	Belgian (Quetelet, Essai, II, p. 23)		Paris (Variot et Chaumet, p. 55)		Toronto (Boas, p. 1547)		Worcester, Mass. (Boas, p. 1548)	
	Height (Boys)	Ann. in- crement	Height		Increment		Varia- bility of do. (6)	
			Boys	Girls	Boys	Girls	Boys	Girls
0	49.6	—	—	—	—	—	—	—
1	69.6	20.0	—	—	—	—	—	—
2	79.7	10.1	74.2	73.6	—	—	—	—
3	86.0	6.3	82.7	81.8	8.5	8.2	—	—
4	93.2	7.2	89.1	88.4	6.4	6.6	—	—
5	99.0	5.8	96.8	95.8	7.7	7.4	105.9	4.4
6	104.6	5.6	103.3	101.9	6.5	6.1	111.6	4.6
7	111.2	6.6	109.9	108.9	6.6	7.0	116.8	4.9
8	117.0	5.8	114.4	113.8	4.5	4.9	122.0	5.2
9	122.7	5.7	119.7	119.5	5.3	5.7	126.9	5.5
10	128.2	5.5	125.0	124.7	5.3	4.8	131.8	5.7
11	132.7	4.5	130.3	129.5	5.3	5.2	136.2	6.2
12	135.9	3.2	133.6	134.4	3.3	4.9	140.7	4.5
13	140.3	4.4	137.6	141.5	4.0	7.1	146.0	7.5
14	148.7	8.4	145.1	148.6	7.5	7.1	152.4	8.5
15	155.9	7.2	153.8	152.9	8.7	4.3	159.7	8.8
16	161.0	5.1	159.6	164.2	5.8	1.3	164.9	5.2
17	167.0	6.0	—	—	—	—	168.9	7.2
18	170.0	3.0	—	—	—	—	171.1	6.7
19	170.6	0.6	—	—	—	—	—	—
20	171.1	0.5	—	—	—	—	—	—

length or stature, and in short that infant, boy and man are not *similar figures**. The change of form seems slight and gradual, but behind it lie other and more complex things. The changing ratio between height and weight implies changes in the child's *metabolism*, in the income and expenditure of the body. The infant stores up fat, and the active child "runs it off" again; at four years old or five, bodily metabolism and increase of weight are at a minimum; but a fresh start is made, a new "nutritional period" sets in, and the small schoolboy grows stout and strong†.

Our curve of growth shews at successive epochs of time the height or weight which has been reached by then; it plots changing magnitude (y) against advancing time (x). It is essentially a *cumulative* or *summation* curve; it sums up or "integrates" all the successive magnitudes which have been added in all the foregoing intervals of time. Where the curve is steep it means that growth was rapid, and when growth ceases the curve becomes a horizontal line. It follows that, by measuring the *slope* or steepness of our curve of growth at successive epochs, we shall obtain a picture of the successive *velocities* or *growth-rates*.

The steepness of a curve is measured by its "gradient‡," or we may roughly estimate it by taking for equal intervals of time (strictly speaking, for each infinitesimal interval of time) the increment added during that interval; and this amounts in practice to taking the *differences* between the values given for the successive epochs, or ages, which we have begun by studying. Plotting these successive differences against time, we obtain a curve each point on which represents a certain rate at a certain time; and while the former curve shewed a continuous succession of varying *magnitudes*, this shews a succession of varying *velocities*. The mathematician calls it a *curve of first differences*; we may call it a curve of annual (or other) increments; but we shall not go wrong if we call it a curve of the *rate (or rates) of growth*, or still more simply, a *velocity-curve*.

* According to Quetelet's data, man's stature is multiplied by 3·4 and his weight by 20·3, between birth and the age of twenty-one. But the cube of 3·4 is nearly 40; so the weight at birth should be multiplied forty times by the age of twenty-one, if infant, boy and man were *similar figures*.

† Cf. T. W. Adams and E. P. Poulton, Heat production in man, *Guy's Hospital Reports* (4), xvii, 1937, and works quoted therein.

‡ That is, by its trigonometrical tangent, referred to the base-line.

We have now obtained two different but closely related curves, based on the selfsame facts or observations, and illustrating them in different ways. One is the inverse of the other; one is the *integral* and one the *differential* of the other; and each makes clear to the eye phenomena which are implicit, but are less conspicuous, in the other. We are using mathematical terms to describe or designate them; but these "curves of growth" are more complicated than the curves with which mathematicians are wont to deal. In our study of growth we may well hope to find curves simpler than these;

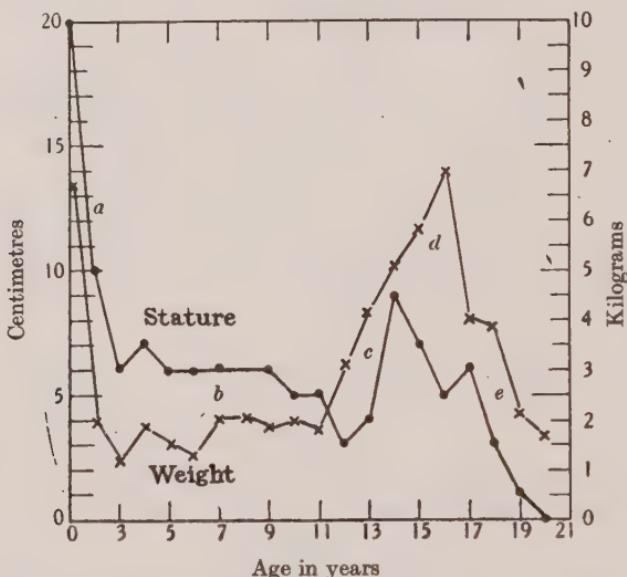


Fig. 5. Annual increments of growth in man. From Quetelet's Belgian data.

but in the successive annual increments of a boy's growth (as Fig. 5 exhibits them) we are dealing with no one continuous operation (such as a mathematical formula might define), but with a *succession of events*, changing as times and circumstances change.

Our curve of increments, or of first differences, for man's stature (Fig. 5) is based, perforce, on annual measurements, and growth alters quickly enough at certain ages to make annual intervals unduly long; nevertheless our curve shews several important things. It suffices to shew, for length or stature, that the growth-rate in early infancy is such as is never afterwards re-attained. From this high early velocity the rate on the whole falls away, until growth itself

comes to an end *; but it does so subject to certain important changes and interruptions, which are much the same whether we draw them from Quetelet's Belgian data, or from the British, American and other statistics of later writers. The curve falls fast and steadily during the first couple of years of the child's life (*a*). It runs nearly level during early boyhood, from four or five years old to nine or ten (*b*). Then, after a brief but unmistakable period of depression † during which growth slows down still more (*c*), the boy enters on

Annual increments of stature and of weight in man
(After Quetelet; see Table, p. 90)

Age	Stature (cm.)		Weight (kgm.)	
	Male	Female	Male	Female
0- 1	20	21	6.8	6.4
1- 2	10	9	2.0	1.9
2- 3	6	7	1.2	1.1
3- 4	7	6	1.9	1.7
4- 5	6	6	1.6	1.3
5- 6	6	6	1.3	1.2
6- 7	6	7	2.1	1.7
7- 8	6	4	2.1	1.4
8- 9	6	6	1.8	2.6
9-10	5	5	2.0	1.8
10-11	5	3	1.7	2.0
11-12	3	5	3.2	4.3
12-13	4	6	4.3	4.1
13-14	9	6	5.2	3.5
14-15	7	2	5.9	3.2
15-16	5	3	7.0	2.1
16-17	6	4	4.0	4.6
17-18	3	2	3.9	4.0
18-19	1	1	2.1	1.4
19-20	0	0	1.7	—

his teens and begins to "grow out of his clothes"; it is his "growing age", and comes to its height when he is about thirteen or fourteen years old (*d*). The lad goes on growing in stature for some years more, but the rate begins to fall off (*e*), and soon does so with great rapidity.

The corresponding curve of increments in weight is not very different from that for stature, but such differences as there are

* As Haller observed it to do in the chick: "Hoc iterum incrementum miro ordine distribuitur, ut in principio incubationis maximum est; inde perpetuo minuatur" (*Elementa Physiologiae*, VIII, p. 294). Or as Bichat says, "Il y a surabondance de vie dans l'enfant" (*Sur la Vie et la Mort*, p. 1).

† This depression, or slowing down before puberty, seems to be a universal phenomenon, common to all races of men. It is a curious thing that Quetelet's "adjusted figures" (which I used in my first edition) all but smooth out of recognition this characteristic feature of his own observations.

between them are significant enough. There is some tendency for growth in weight to fall off or fluctuate at four or five years old, before the small boy goes to school; but there is, or should be, little retardation of weight when growth in height slows down before he enters on his teens*. The healthy lad puts on weight again more and more rapidly, for some little while after growth in stature has slowed down; and normal increase of weight goes on, more slowly, while the man is "filling out," long after growth in stature has come to an end. But somewhere about thirty he begins losing weight a little; and such subsequent slow changes as men commonly undergo we need not stop to deal with.

The differences in stature and build between one race and another are in like manner a question of growth-rate in the main. Let us take a single instance, and compare the annual increments of growth in Chinese and English boys. The curves are much the same in form, but differ in amplitude and phase. The English boy is growing faster all the while; but the minimal rate and the maximal rate come later by a year or more than in the Chinese curve† (Fig. 6).

Quetelet was not the first to study man's growth and stature, nor was he the first student of social statistics and "demography." The foundations of modern vital statistics had been laid by Graunt and Petty in the seventeenth century‡; the economists developed the subject during the eighteenth§, and parts of it were studied

* That the annual increments of weight in boys are nearly constant, and the curve of growth nearly a straight line at this age, especially from about 8 to 11, has been repeatedly noticed. Cf. Elderton, Glasgow School-children, *Biometrika*, x, p. 283, 1914-15; Fessard and others, *Croissance des Ecoliers Parisiens*, 1934, p. 13. But careful measurements of American children, by Katherine Simmons and T. Wingate Todd, shew steadily increasing increments from four years old till puberty (*Growth*, II, pp. 93-133, 1938).

† For copious bibliography, see J. Needham, *op. cit.*, also Gaston Backman, Das Wachstum der Körperlänge des Menschen, *K. Sv. Vetensk. Akad. Hdlgr.* (3), XIV, 1934.

‡ Cf. John Graunt's *Natural and Political Observations... upon the Bills of Mortality*, London, 1662; *The Economic Writings of Sir William Petty*, ed. by C. H. Hull, 2 vols., Cambridge, Mass., 1927. Concerning Graunt and Petty—two of the original Fellows of the Royal Society—see (*int. al.*) H. Westergaard, *History of Statistics*, 1932, and L. Hogben (and others), *Political Arithmetic*, 1938.

§ Besides the many works of the economists, cf. J. G. Roederer, *Sermo de pondere et longitudine recens-natorum*, *Comment. Soc. Reg. Sci. Gottingae*, III, 1753; J. F. G. Dietz, *De temporum in graviditate et partu aestimatione*, Diss., Göttingen, 1757.

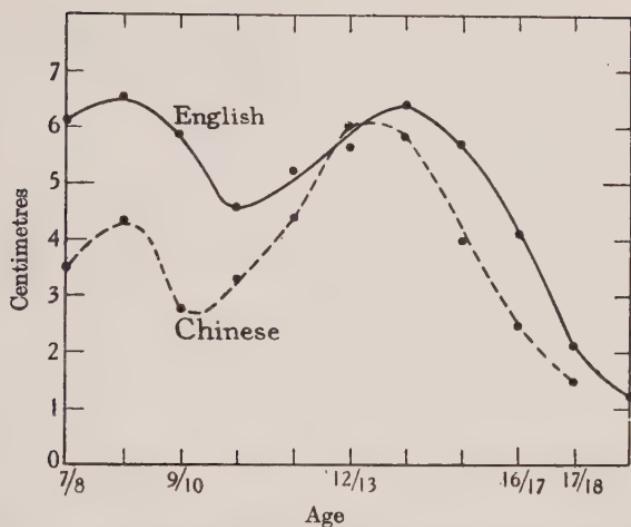


Fig. 6. Annual increments of stature. From Roberts' (English) and Appleton's (Chinese) data.

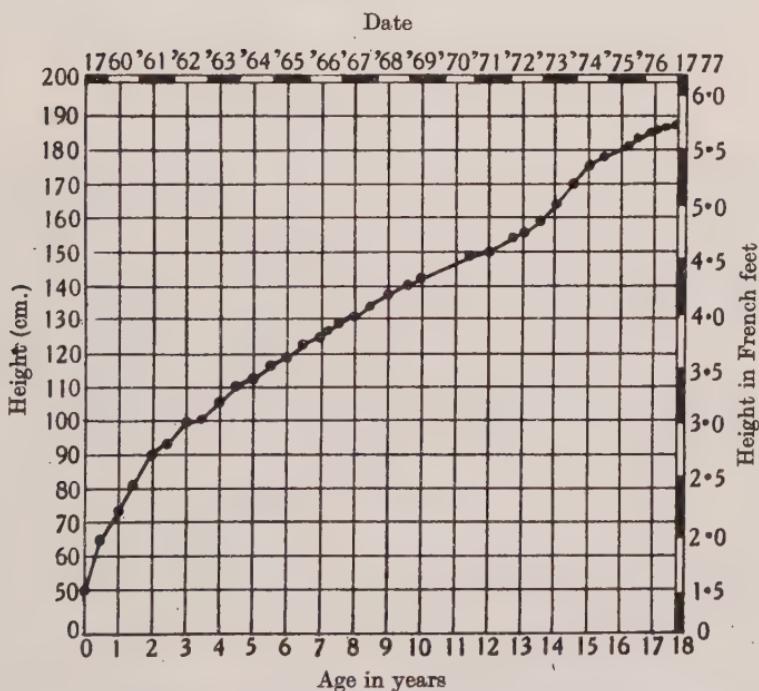


Fig. 7. Curve of growth of a French boy of the eighteenth century. From Scammon, after Buffon.

eagerly in the early nineteenth, when the exhaustion of the armies of France and the evils of factory labour in England drew attention to the stature and physique of man and to the difference between the healthy and the stunted child*.

A friend of Buffon's, the Count Philibert Guéneau de Montbeillard, kept careful measurements of his own son; and Buffon published these in 1777, in a supplementary volume of the *Histoire Naturelle*†. The child was born in April 1759; it was measured every six months

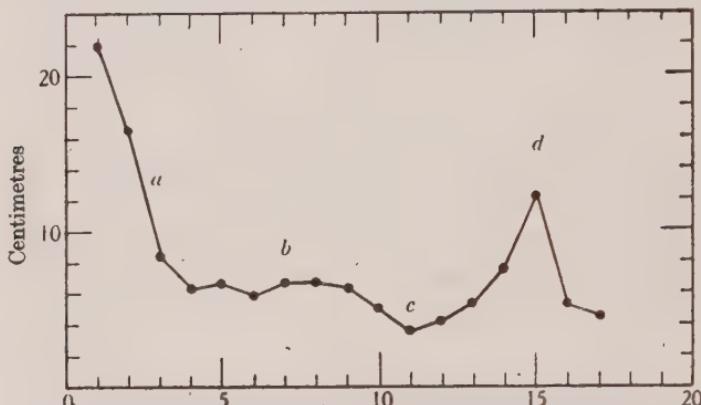


Fig. 8. Annual increments of stature of the said French boy.

for seventeen years, and the record gives a curve of great interest and beauty (Fig. 7). There are two ways of studying such a phenomenon—the statistical method based on large numbers, and the careful study of the individual case; the curve of growth of this one French child is to all intents and purposes identical, save that the boy was throughout a trifle taller, with the mean curve yielded by a recent study of forty-four thousand little Parisians‡.

In young Montbeillard's case the "curve of first differences," or of the successive annual increments of stature (Fig. 8), is clear and beautiful. It shews (a) the rapid, but rapidly diminishing, rate of

* Cf. M. Hargenvilliers, *Recherches... sur... le recrutement de l'armée en France*, 1817; J. W. Cowell, Measurements of children in Manchester and Stockport, *Factory Reports*, I; and works referred to by Quetelet.

† See Richard E. Scammon, The first seriatim study of human growth, *Amer. Journ. of Physical Anthropology*, x, pp. 329–336, 1927.

‡ MM. Variot et Chaumet, Tables de croissance, dressées... d'après les mensurations de 44,000 enfants parisiens, *Bull. et Mém. Soc. d'Anthropologie*, III, p. 55, 1906.

growth in infancy; (b) the steady growth in early boyhood; (c) the period of retardation which precedes, and (d) the rapid growth which accompanies, puberty.

Buffon, with his usual wisdom, adds some remarks of his own, which include two notable discoveries. He had observed that a man's stature is measurably diminished by fatigue, and the loss soon made up for in repose; long afterwards Quetelet said, to the same effect, "le lit est favorable à la croissance, et le matin un homme est un peu plus grand que le soir." Buffon asked whether growth varied with the seasons, and Montbeillard's data gave him his reply. Growth was quicker from April to October than during the rest of the year: shewing that "la chaleur, qui agit généralement sur le développement de tous les êtres organisées, influe considérablement sur l'accroissement du corps humain." Between five years old and ten, the child grew seven inches during the five summers, but during the five winters only four; there was a like difference again, though not so great, while the boy was growing quickly in his teens; but there were no seasonal differences at all from birth to five years old, when the child was doubtless sheltered from both heat and cold*.

On rate of growth in man and woman

That growth follows a different course in boyhood and in girlhood is a matter of common knowledge; but differences in the curves of growth are not very apparent on the scale of our diagrams. They are better seen in the annual increments, or first differences; and we may further simplify the comparison by representing the girl's weight or stature as a *percentage* of the boy's.

Taking weight to begin with (Fig. 9), the girl's growth-rate is steady in childhood, from two or three to six or seven years old,

* Growth-rates based on the continuous study of a single individual are rare; we depend mostly on average measurements of many individuals grouped according to their average age. That this is a sound method we take for granted, but we may lose by it as well as gain. (See above, p. 92.) The chief epochs of growth, the chief singularities of the curve, will come out much the same in the individual and in the average curve. But if the individual curves be skew, averaging them will tend to smooth the skewness away; and, more curiously, if they be all more or less diverse, though all symmetrical, a certain skewness will tend to develop in the composite or average curve. Cf. Margaret Merrill, *The relationship of individual to average growth*, *Human Biology*, III. pp. 37-70, 1931.

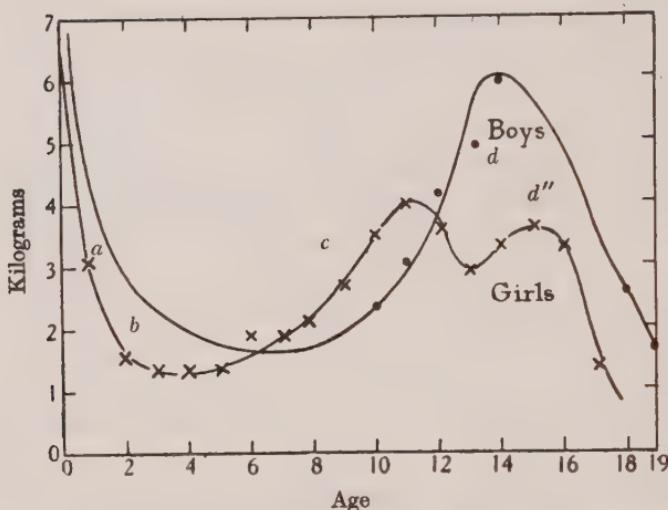


Fig. 9. Annual increase in weight of Belgian boys and girls.
From Quetelet's data. (Smoothed curves.)

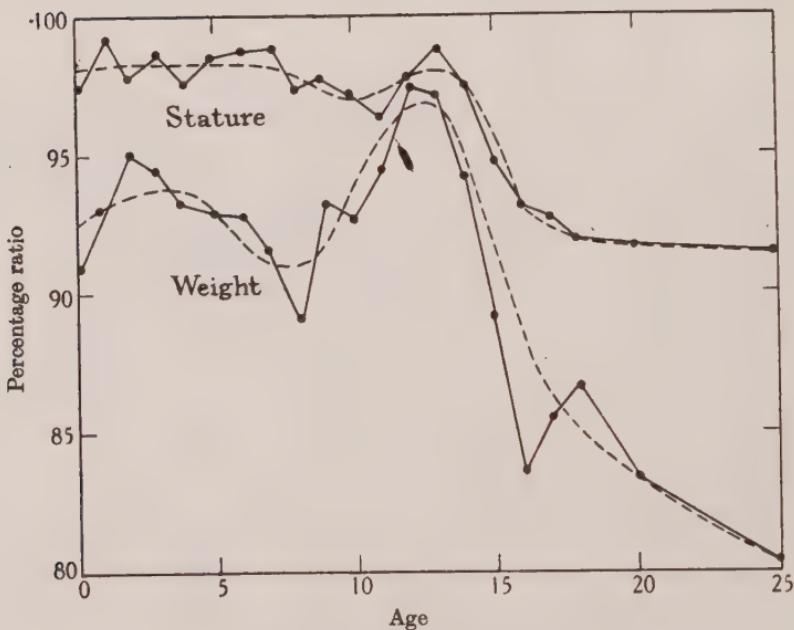


Fig. 10. Percentage ratio of female weight and stature to male.
From Quetelet's Belgian data.

just as is the boy's; but her curve stands on a lower level, for the little maid is putting on less weight than the boy (*b*). Later on, her rate accelerates (*c*) sooner than does his, but it never rises quite so high (*d*). After a first maximum at eleven or twelve her rate of growth slows down a little, then rises to a second maximum when

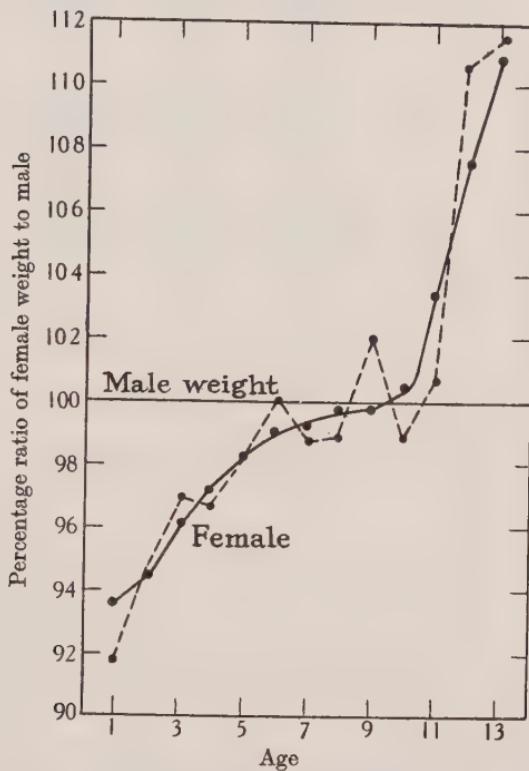


Fig. 11. Relative weight of American boys and girls..
From Simmons and Todd's data.

she is sixteen or seventeen, after the boy's phase of quickest growth is over and done. This second spurt of growth, this increase of vigour and of weight in the girl of seventeen or eighteen, Quetelet's figures indicate and common observation confirms. Last of all, while men stop adding to their weight about the age of thirty or before, this does not happen to women. They increase in weight, though slowly, till much later on: until there comes a final phase, in both sexes alike, when weight and height and strength decline together.

Stature of school children, Welsh and English. (From R. M. Fleming's data)

Age	Stature (cm.)			Annual increment (cm.)			Coefficient of variability of stature		
	Boys	Girls	Difference	Percentage difference			Boys	Girls	Difference
				Boys	Girls	Difference			
3	96.3	96.0	0.3	99.7	6.5	5.6	0.9	86.1	5.44
4	102.8	101.6	1.2	98.7	5.4	6.4	-1.0	118.5	5.27
5	108.2	108.0	1.2	99.8	4.8	5.8	-1.0	120.8	5.09
6	113.0	113.8	-0.8	100.7	5.1	4.1	1.0	80.4	5.41
7	118.1	117.9	0.2	99.8	5.6	5.5	0.1	98.2	4.97
8	123.7	123.4	0.3	99.7	4.3	4.4	-0.1	102.3	5.32
9	128.0	127.8	0.2	99.9	4.3	4.8	-0.5	111.6	5.45
10	132.3	132.6	-0.3	100.2	4.4	5.3	-0.9	120.4	5.58
11	136.7	137.9	-1.2	100.8	5.3	6.1	-0.8	115.1	5.70
12	142.0	144.0	-2.0	101.2	6.1	5.6	0.5	91.8	5.55
13	148.1	149.6	-1.5	101.0	7.6	5.1	2.5	67.1	5.81
14	155.7	154.7	1.0	99.4	7.6	3.5	4.1	46.0	5.78
15	163.3	158.2	5.1	96.9	5.1	1.3	3.8	25.5	5.82
16	168.4	159.5	8.9	94.7	3.1	0.8	2.3	4.96	3.92
17	171.5	160.3	11.2	93.5	1.0	0.5	0.5	4.30	3.72
18	172.5	160.8	11.7	93.3	1.7	0.5	0.5	2.95	3.85

Stature and weight of American children (Ohio)
(From Katherine Simmons and T. Wingate Todd's data)

Age	Stature (cm.)			Weight (lbs.)		
	Boys	Girls	% ratio	Boys	Girls	% ratio
3 months	61.3	59.3	96.7	14.4	13.1	91.1
1 year	76.1	74.2	97.5	23.9	21.9	91.8
2 "	87.4	86.2	98.6	29.1	27.5	94.7
3 "	96.2	95.5	99.3	33.5	32.5	96.9
4 "	103.9	103.2	99.3	38.4	37.1	96.7
5 "	110.9	110.3	99.4	43.2	42.3	98.1
6 "	117.2	117.4	100.1	48.5	48.6	100.0
7 "	123.9	123.2	99.4	54.7	54.0	98.8
8 "	130.1	129.3	99.4	62.2	61.5	98.7
9 "	136.0	135.7	99.7	69.5	70.9	102.0
10 "	141.4	140.8	99.6	78.5	77.6	98.8
11 "	146.5	147.8	100.7	86.5	87.0	100.6
12 "	151.1	155.3	102.8	92.7	102.7	110.7
13 "	156.7	159.9	102.0	102.8	114.6	111.4

Mean of observed increments of stature and weight of American children

Age	Increment of stature (mm.)			Increment of weight (lbs.)		
	Boys	Girls	% ratio	Boys	Girls	% ratio
3 m. - 1 yr.	150.4	150.1	99.8	9.32	8.07	93.8
1 yr. - 2 "	123.9	132.0	106.5	4.97	5.56	112.0
2 " - 3 "	88.1	90.0	102.2	4.01	4.18	104.3
3 " - 4 "	73.9	79.1	106.9	4.13	4.46	108.0
4 " - 5 "	69.4	72.2	104.0	4.60	4.55	99.8
5 " - 6 "	67.0	68.0	101.5	4.51	5.08	112.8
6 " - 7 "	64.1	62.6	97.6	5.57	5.40	96.9
7 " - 8 "	61.2	57.8	94.4	6.70	6.65	99.4
8 " - 9 "	55.7	60.1	108.0	6.64	7.38	111.1
9 " - 10 "	54.9	57.7	105.1	7.92	8.12	104.8
10 " - 11 "	51.9	61.3	118.2	8.81	9.58	108.7
11 " - 12 "	53.2	66.9	125.6	9.54	11.98	133.1
12 " - 13 "	61.0	55.1	89.0	10.90	10.29	94.7

These differences between the two sexes, which are essentially *phase-differences*, cause the *ratio* between their weights to fluctuate in a somewhat complicated way (Figs. 10, 11). At birth the baby girl's weight is about nine-tenths of the boy's. She gains on him for a year or two, then falls behind again; from seven or eight onwards she gains rapidly, and the girl of twelve or thirteen is very little lighter than the boy; indeed in certain American statistics she is by a good deal the heavier of the two. In their teens the boy gains

steadily, and the lad of sixteen is some 15 per cent. heavier than the lass. The disparity tends to diminish for a while, when the maid of seventeen has her second spurt of growth; but it increases again, though slowly, until at five-and-twenty the young woman is no more than four-fifths the weight of the man. During middle life she gains on him, and at sixty the difference stands at some 12

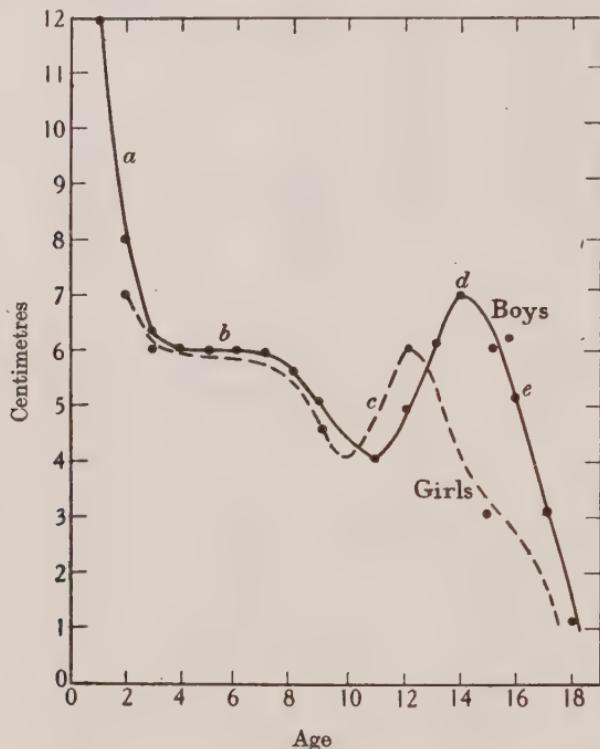


Fig. 12. Annual increments of stature, in boys and girls.
From Quetelet's data. (Smoothed curves.)

per cent., not far from the mean for all ages; but the old woman shrinks and dwindle, and the difference tends to increase again.

The rate of increase of stature, like stature itself, differs notably in the two sexes, and the differences, as in the case of weight, are mostly a question of *phase* (Fig. 12). The little girl is adding rather more to her stature than the boy at four years old *, but she grows

* This early spurt of growth in the girl is shewn in English, French and American observations, but not in Quetelet's.

slower than he does for a few years thereafter (*b*). At ten years old the girl's growth-rate begins to rise (*c*), a full year before the boy's; at twelve or thirteen the rate is much alike for both, but it has reached its maximum for the girl. The boys' rate goes on rising, and at fourteen or fifteen they are growing twice as fast as the girls. So much for the annual increments, as a rough measure of the *rates* of growth. In actual stature the baby girl is some 2 or 3 per cent. below the boy at birth; she makes up the difference, and there is

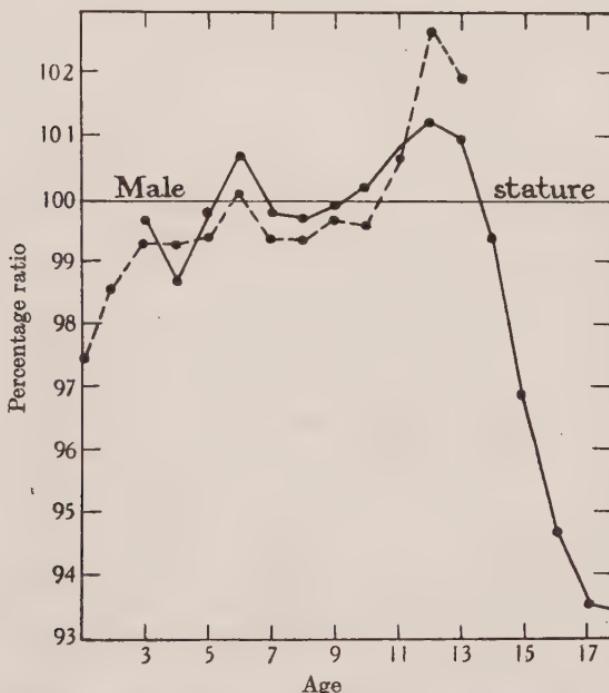


Fig. 13. Ratio of female stature to male. —— From R. M. Fleming's data.
- - - - From Simmons and Todd's data.

good evidence to shew that she is by a very little the taller for a while, at about five years old or six. At twelve or thirteen she is very generally the taller of the two, and we call it her "gawky age" (Fig. 13).

Man and woman differ in length of life, just as they do in weight and stature. More baby boys are born than girls by nearly 5 per cent. The numbers draw towards equality in their teens; after

twenty the women begin to outnumber the men, and at eighty-five there are twice as many women as men left in the world*

Men have pondered over the likeness and the unlikeness between the short lifetimes and the long; and some take it to be fallacious to measure all alike by the common timepiece of the sun. Life, they say, has a varying time-scale of its own; and by this modulus the sparrow lives as long as the eagle and the day-fly as the man†. The time-scale of the living has in each case so strange a property of logarithmic decrement that our days and years are long in childhood, but an old man's minutes hasten to their end.

On pre-natal and post-natal growth

The rates of growth which we have so far studied are based on annual increments, or "first differences" between yearly determinations of magnitude. The first increment indicates the *mean rate* of growth during the first year of the infant's life, or (on a further assumption) the mean rate at the mean epoch of six months old; there is a gap between that epoch and the epoch of birth, of which we have learned nothing; we do not yet know whether the very high rate shewn within the first year goes on rising, or tends to fall, as the date of birth is approached. We are accustomed to interpolate freely, and on the whole safely, *between* known points on a curve: "si timide que l'on soit, il faut bien que l'on interpole;" says Henri Poincaré; but it is much less safe and seldom justifiable (at least until we understand the physical principle involved and its mathematical expression) to "extrapolate" beyond the limits of our observations.

We must look for more detailed observations, and we may learn much to begin with from certain old tables of Russow's‡, who gives

* Cf. F. E. A. Crew's Presidential Address to Section D of the British Association, 1937.

† Cf. Gaston Backman, Die organische Zeit, *Lunds Universitets Årsskrift*, xxxv, Nr. 7, 1939.

‡ Quoted in Vierordt's *Anatomische...Daten und Tabellen*, 1906, p. 13. See also, among many others, Camerer's data, in Pfaundler and Schlossman's *Hdb. d. Kinderheilkunde*, I, pp. 49, 424, 1908; Variot, *op. cit.*; for pre-natal growth, R. E. Scammon and L. A. Calkins, *Growth in the Foetal Period*, Minneapolis, 1929. Also, on this and many other matters, E. Fauré-Fremiet, *La cinétique du développement*, Paris, 1925; and, not least, J. Needham, *Chemical Embryology*, 1931.

Differences between boy and girl in annual increments of stature

Years of Age	...	1/2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
Belgian (Quetelet)	1.0	1.0	1.0	0.0	0.0	1.0	2.0	0.0	0.0	2.0	2.0	3.0	5.0	2.0	2.0	1.0	—	—	—	—
British (Fleming)	—	—	0.9	1.0	1.0	0.1	0.1	0.1	0.5	0.9	0.8	0.5	2.5	4.1	3.8	2.3	—	—	—	—
Parisian (Variot)	0.3	0.2	0.3	0.1	0.4	0.4	0.4	0.5	0.5	0.1	1.6	3.1	0.4	4.4	4.5	—	—	—	—	—
New England (Boas and Wissler)	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—

Or we may take (among many others) certain careful measurements of Parisian children*, as follows:—

Months after birth	...	0	1	2	3	4	5	6	7	8	9	10	11	12
Stature (cm.)	Bcys	49.8	53.1	56.6	58.7	61.1	62.8	64.7	66.0	67.0	68.3	69.5	70.4	71.8
	Girls	49.3	52.9	55.8	57.7	60.5	61.8	63.8	65.2	66.0	67.7	69.1	70.3	71.5
Weight (kgm.)	Boys	3.13	3.62	4.32	4.93	5.71	6.21	6.68	7.15	7.65	8.01	8.53	8.78	9.03
	Girls	3.02	3.55	4.23	4.80	5.40	5.99	6.51	6.92	7.46	7.81	8.30	8.70	8.96
Increments of Stature (cm.)	Boys	—	3.3	3.5	2.1	2.4	1.7	1.9	1.3	1.0	1.3	1.2	0.9	1.4
	Girls	—	3.6	2.9	1.9	2.8	1.3	2.0	1.4	0.8	1.7	1.4	1.2	1.2
Weight (kgm.)	Boys	—	4.9	7.0	6.1	7.8	5.0	4.7	4.7	5.0	3.6	5.2	2.5	2.5
	Girls	—	4.3	6.8	5.7	6.0	5.9	5.2	4.1	5.4	3.5	4.9	4.0	2.6
Percentage ratio of boys to girls	Stature	101.3	100.3	101.4	101.6	101.0	101.5	101.4	101.2	101.4	101.0	100.5	100.1	100.4
	Weight	103.6	101.5	102.1	102.7	105.8	103.7	102.6	103.3	102.6	101.5	102.8	101.0	100.7

* From G. Variot, *La Croissance chez le nourrisson*, 1925, p. 119.

the stature of the infant, month by month, during the first year of its life, as follows:

*Mean growth of an infant, in its first twelve-month
(After Russow)*

Age (months)	0	1	2	3	4	5	6	7	8	9	10	11	12
Length (cm.)	50	54	58	60	62	64	65	66	67.5	68	69	70.5	72
Monthly incre- ment (cm.)	—	4	4	2	2	2	1	1	1.5	0.5	1	1.5	1.5

From these data of Russow's for German children, rough as indeed they are, from Variot's for little Parisians (Fig. 14), and from

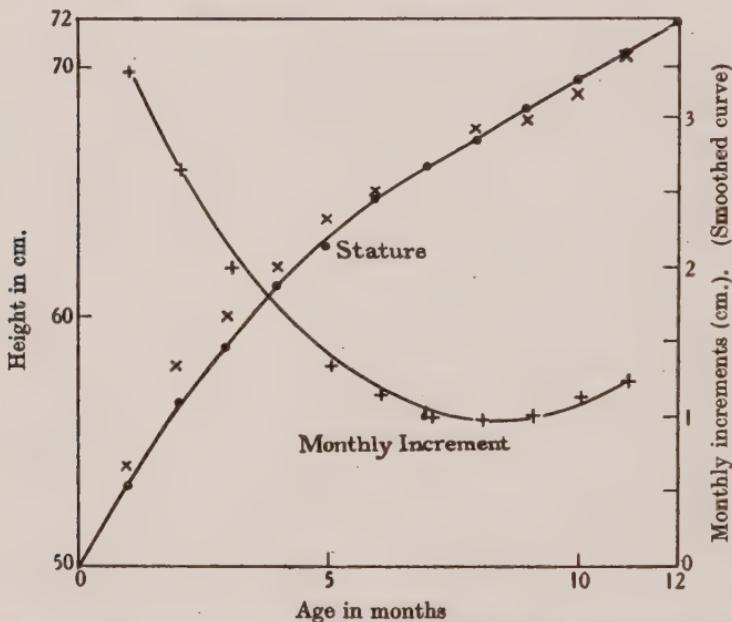


Fig. 14. Growth of Parisian children (boys) from birth to twelve months old.
From G. Variot's data; Russow's German data are also shewn, by $\times \times \times$.

many more, we see that the rate of growth rises steadily and even rapidly as we pass backwards towards the date of birth. It is never anything like so great again. It is an impressive demonstration of the dynamic potentiality, of the store of energy, in the newborn child.

But birth itself is but an incident, an inconstant epoch, in the life and growth of a viviparous animal. The foal and the lamb

are born later than a man-child; the puppy and the kitten are born earlier, and in more helpless case than ours; the mouse comes into the world still earlier and more inchoate, so much so that even the little marsupial is scarcely more embryonic and unformed*. We must take account, so far as each case permits, of pre-natal or intra-uterine growth, if we are to study the curve of growth in its entirety.

According to His†, the following are the mean lengths from month to month of the unborn child:

Months	0	1	2	3	4	5	6	7	8	9	10 (Birth)
Length (mm.)	0	7.5	40	84	162	275	352	402	443	472	490} 500}
Increment per month (mm.)	—	7.5	32.5	44	78	113	77	50	41	29	18} 28}

These data link on very well to those of Russow, which we have just considered; and (though His's measurements for the prenatal months are more detailed than are those of Russow for the first year of post-natal life) we may draw a continuous curve of growth (Fig. 15) and of increments of growth (Fig. 16) for the combined periods. It will be seen at once that there is a "point of inflection" somewhere about the fifth month of intra-uterine life; up to that date growth proceeds with a continually increasing velocity. After that date, though growth is still rapid, its velocity tends to fall away; the curve, while still ascending, is becoming an S-shaped curve (Fig. 15). There is a slight break between our two sets of statistics at the date of birth, an epoch regarding which we should like to have precise and continuous information. But we can see that there is undoubtedly a certain slight arrest of growth, or diminution of the rate of growth, about this epoch; the sudden change of nurture has its inevitable effect, but this slight tem-

* It is part of the story, though by no means all, that (as Minot says) the larger the litter the sooner does birth take place. That the day-old foal or fawn can keep pace with their galloping dams is very remarkable; it is usually explained teleologically, as a provision of Nature, on which their safety and their survival depend. But the fact that they come one at a birth has at least something to do with their comparative maturity.

† *Unsere Körperform und das physiologische Problem ihrer Entstehung*, Leipzig, 1874. On growth in weight of the human embryo, see C. M. Jackson, *Amer. Journ. Anat.* xvii, p. 118, 1909; also J. Needham, *op. cit.* pp. 379-383.

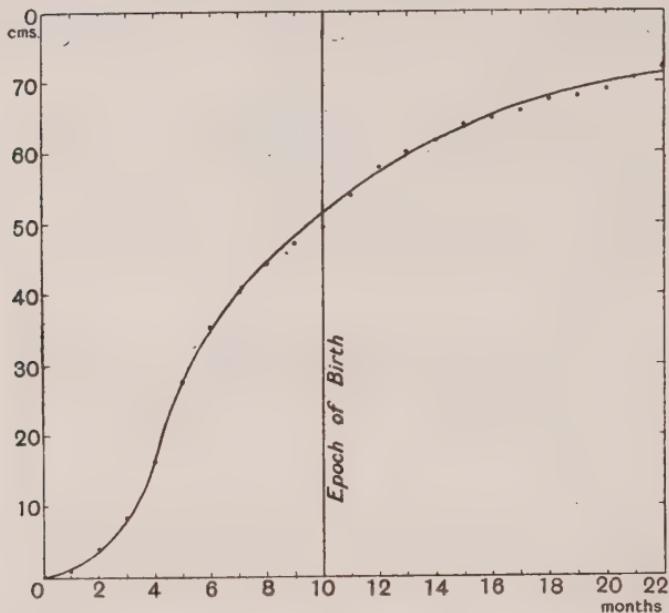


Fig. 15. Curve of growth (in length or stature) of child, before and after birth.
From His and Russow's data.

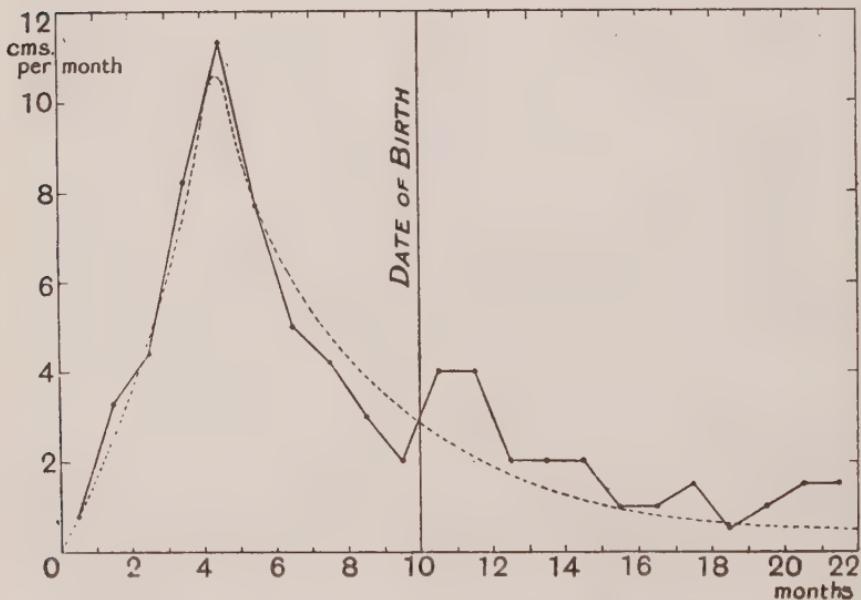


Fig. 16. Mean monthly increments of length or stature of child, in cm.
From His and Russow's data.

porary set-back is immediately followed by a secondary, and equally transitory, acceleration*.

Mean weight in grams of American infants during ten days after birth. (From Meredith and Brown)

Age (days)	Weight		Daily increment	
	Male	Female	Male	Female
At birth	3491	3408	—	—
1	3376	3283	- 115	- 125
2	3294	3207	- 82	- 76
3	3274	3195	- 20	- 12
4	3293	3213	19	17
5	3326	3246	33	34
6	3366	3281	40	35
7	3396	3315	30	34
8	3421	3341	25	26
9	3440	3362	19	21
10	3466	3387	26	25

The set-back after birth of which we have just spoken is better shewn by the child's weight than by any linear measurement. During its first three days the infant loses weight visibly, and it is more than ten days old before it has made up the weight it lost in those first three (Fig. 17).

It is worth our while to illustrate on a larger scale His's careful data for the ten months of pre-natal life (Fig. 18). They give an S-shaped curve, beautifully regular, and nearly symmetrical on either side of its point of inflection; and its differential, or curve of monthly increments, is a bell-shaped curve which indicates with the utmost simplicity a rise from a minimal to a maximal rate, and a fall to a minimum again. It has a close family likeness to the well-known "curve of probability," of which we shall presently have much more to say; it is a curve for which we might well hope to find a simple mathematical expression†.

These two curves, then, look more "mathematical," and less merely descriptive, than any others we have yet drawn, and much

* See especially, H. V. Meredith and A. W. Brown, Growth in body-weight during first ten days of postnatal life, *Human Biology*, xi, pp. 24-77, 1939. Also (int. al.) T. Brailsford Robertson, Pre- and post-natal growth, etc., *Amer. Journ. Physiol.* xxxvii, pp. 1-42, 74-85, 1915.

† The same is not less true of Friedenthal's more elaborate measurements, in his *Physiologie des Menschenwachstums*, 1914; cf. Needham, *op. cit.* p. 1677.

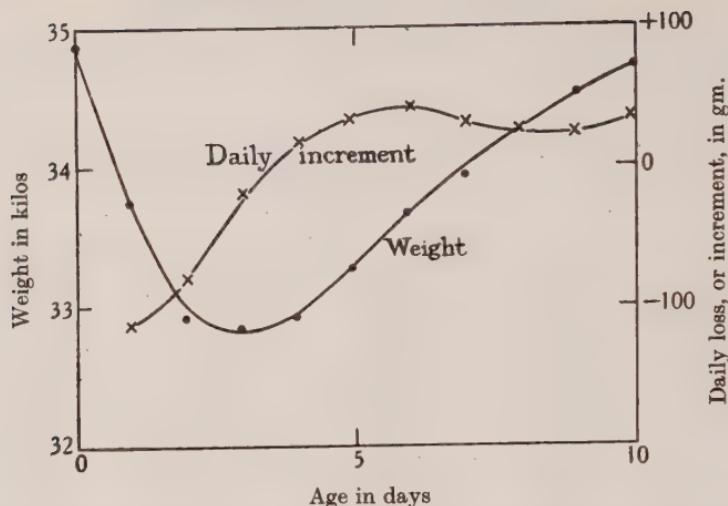


Fig. 17. Mean weight of American infants. From Meredith and Brown's data.

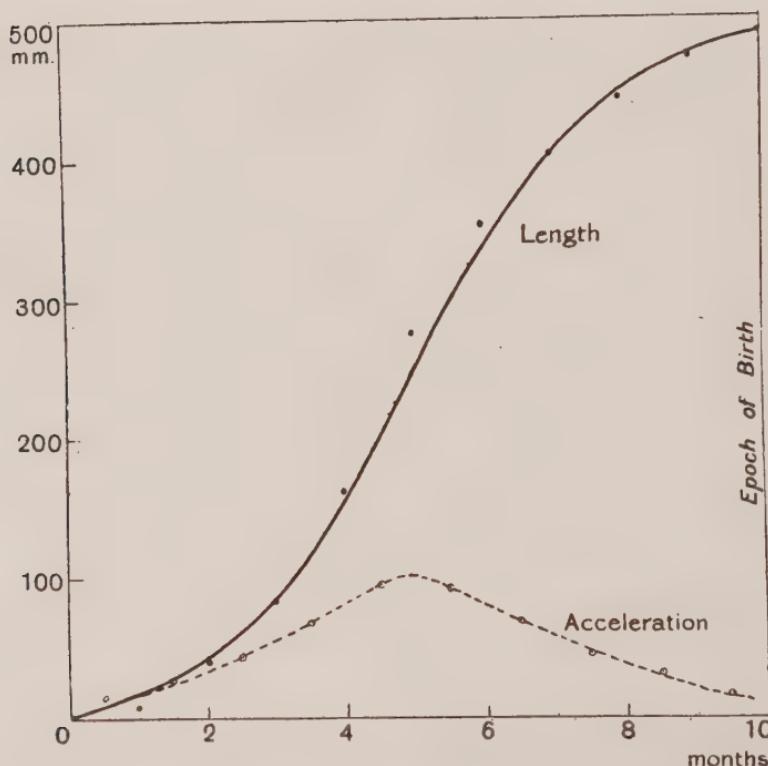


Fig. 18. Curve of a child's pre-natal growth, in length or stature; and corresponding curve of mean monthly increments (mm.). (Smoothed curves.)

the same curves meet us again and again in the growth of other organisms. The pre-natal growth of the guinea-pig is just the same*. We have the same essential features, the same S-shaped curve, in the growth by weight of an ear of maize (Fig. 19), or the growth in length of the root of a bean (Fig. 20); in both we see the same slow beginning, the rate rapidly increasing to a maximum, and the subsequent slowing down or "negative acceleration†." One phase passes into another; so far as these curves go, they exhibit growth as a continuous process, with its beginning, its middle and its end—a continuity which Sachs recognised some seventy years ago, and spoke of as the "grand period of growth‡."

But these simple curves relate to simple instances, to the infant sheltered in the womb, or to plant-growth in the sunny season of the year. They mark a favourable episode, rather than relate the course of a lifetime. A curve of growth to run all life long is only simple in the simplest of organisms, and is usually a very complex affair.

*Growth in length of Vallisneria§, and root of bean||
and weight of maize¶*

<i>Vallisneria</i>		<i>Vicia</i>		<i>Zea</i>	
Hours	Inches	Days	Mm.	Days	Gm.
6	0·3	0	1·0	6	1
16	1·7	1	2·8	18	4
42	12·6	2	6·5	30	9
54	15·4	3	24·0	39	17
65	16·1	4	40·5	46	26
77	16·7	5	57·5	53	42
88	17·1	6	72·0	60	62
		7	79·0	74	71
		8	79·0	93	74

It would seem to be a natural rule, that those offspring which are most highly organised at birth are those which are born largest

* See R. L. Draper, *Anat. Record*, xviii, p. 369, 1920; cf. Needham, *op. cit.*, p. 1672.

† Cf. R. Chodat et A. Monnier; Sur la courbe de croissance chez les végétaux, *Bull. Herbier Boissier* (2), v, p. 615, 1905.

‡ *Arbeiten a. d. bot. Instit. Würzburg*, i, p. 569, 1872.

§ A. Bennett, *Trans. Linn. Soc.* (2), i (Bot.), p. 133, 1880.

|| Sachs, *l.c.*

¶ Stefanowska, *op. cit.*; G. Backman, *Ergebn. d. Physiologie*, xxiii, p. 925, 1931.

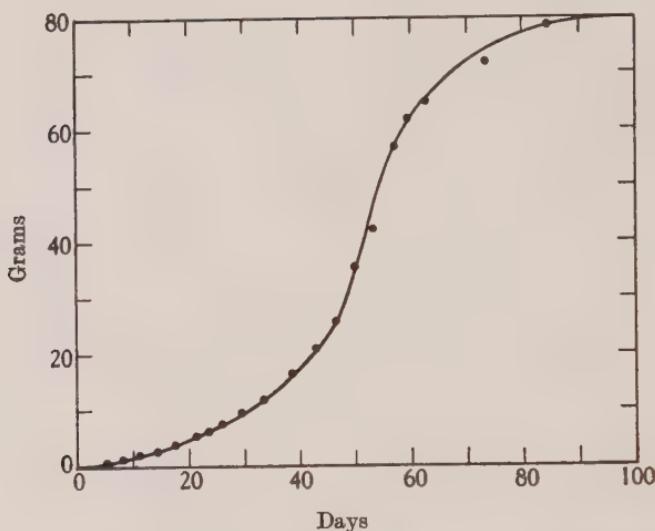


Fig. 19. Growth in weight of maize. From Gustav Backman, after Stefanowska.

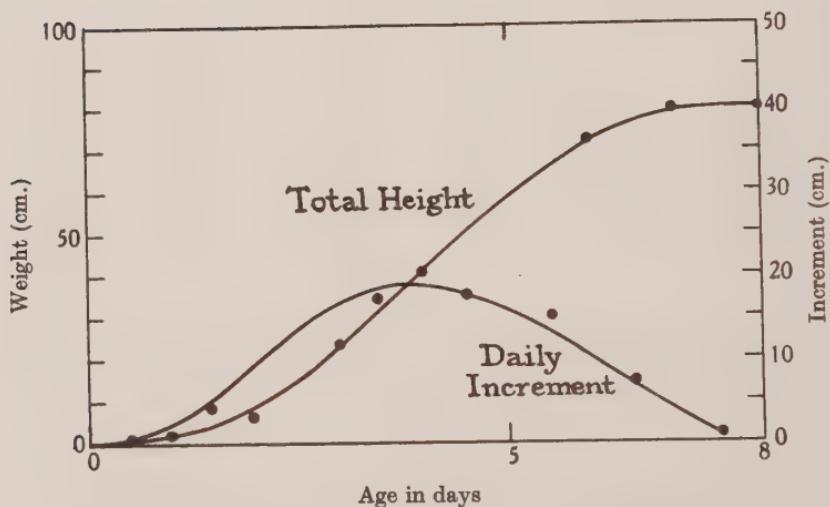


Fig. 20. Growth in height of a beanstalk. From Sachs's data.

relatively to their parents' size. But another rule comes in, which is perhaps less to be expected, that the offspring are born smaller the larger the species to which they belong. Here we shew, roughly, the relative weights of the new-born animal and its mother*:

Bear	1 : 600		Sheep	1 : 14
Lion	180		Ox	13
Hippopotamus	45		Horse	12
Dog	45-50		Rabbit	40
Cat	25		Mouse	10-25
Man	22		Guinea-pig	7

These differences at birth are for the most part made up quickly; in other words, there are great differences in the rate of growth during early post-natal life. Two lion-cubs, studied by M. Anthony, grew as follows:

	Male	Female
Feb. 23 (born)	—	—
28	2·0 kilos	1·7 kilos
Mar. 8	3·0	2·6
15	3·8	3·3
22	4·6	4·0
30	5·3	4·6
Apr. 5	6·1	5·2
12	7·0	6·0
19	8·0	7·0

Thus the lion-cub doubles its weight in the first month, and wellnigh doubles it again in the second; but the newborn child takes fully five months to double its weight, and nearly two years to do so again.

The size finally attained is a resultant of the rate and of the duration of growth; and one or other of these may be the more important, in this case or in that. It is on the whole true, as Minot said, that the rabbit is bigger than the guinea-pig because he grows faster, but man is bigger than the rabbit because he goes on growing for a longer time.

A bantam and a barn-door fowl differ in their rate of growth, which in either case is definite and specific. Bantams have been bred to match almost every variety of fowl; and large size or small, quick growth or slow, is inherited or transmitted as a Mendelian

* Data from Variot, after Anthony.

character in every cross between a bantam and a larger breed. The bantam is not produced by selecting smaller and smaller specimens of a larger breed, as an older school might have supposed; but always by first crossing with bantam blood, so introducing the "character" of smallness or retarded growth, and then segregating the desired types among the dwarfish offspring. In fact, Darwinian selection plays a small and unimportant part in the process*.

From the whole of the foregoing discussion we see that rate of growth is a specific phenomenon, deep-seated in the nature of the organism; wolf and dog, horse and ass, nay man and woman, grow at different rates under the same circumstances, and pass at different epochs through like phases of development. Much the same might be said of mental or intellectual growth; the girl's mind is more precocious than the boy's, and its development is sooner arrested than the man's†.

On variability, and on the curve of frequency or of error

The magnitudes which we are dealing with in this chapter—heights and weights and rates of change—are (with few exceptions) mean values derived from a large number of individual cases. We deal with what (to borrow a word from atomic physics) we may call an *ensemble*; we employ the equalising power of averages, invoke the "law of large numbers‡," and claim to obtain results thereby which are more trustworthy than observation itself§. But in ascertaining a mean value we must also take account of the *amount of variability*, or departure from the mean, among the cases from which the mean value is derived. This leads on far beyond our scope, but we must spare it a passing word; it was this identical phenomenon, in the case of Man, which suggested to Quetelet the

* Cf. Raymond Pearl, The selection problem, *Amer. Naturalist*, 1917, p. 82; R. C. Punnett and P. G. Bailey, *Journ. of Genetics*, iv, pp. 23–39, 1914.

† Cf. E. Devaux, L'allure du développement dans les deux sexes, *Revue génér. des Sci.* 1926, p. 598.

‡ S. D. Poisson, following James Bernoulli's *Ars Conjectandi* (op. posth. 1713), was the discoverer, or inventor, of the law of large numbers. "Les choses de toute nature sont soumises à une loi universelle qu'on peut appeler la loi des grands nombres" (*Recherches*, 1837, pp. 7–12).

§ See p. 137, footnote.

statistical study of Variation, led Francis Galton to enquire into the laws of Natural Inheritance, and served Karl Pearson as the foundation of his science of Biometrics.

When Quetelet tells us that the *mean stature* of a ten-year-old boy is 1.275 metres, this is found to imply, not only that the measurements of all his ten-year-old boys group themselves about this mean value of 1.275 metres, but that they do so *in an orderly way*, many departing little from that mean value, and fewer and fewer departing more and more. In fact, when all the measurements are grouped and plotted, so as to shew the number of instances (y) at each gradation of size (x), we obtain a characteristic

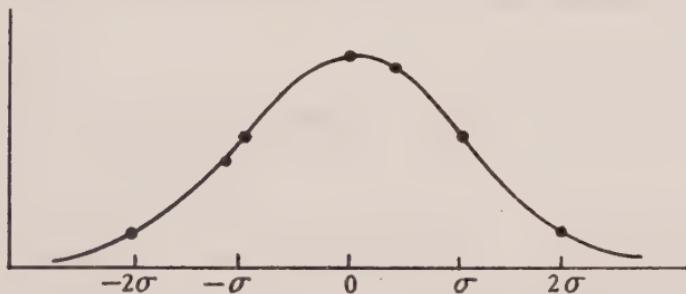


Fig. 21. The normal curve of frequency, or of error.
 σ , $-\sigma$, the "standard deviation".

configuration, mathematically definable, called the *curve of frequency*, or of *error* (Fig. 21). This is a very remarkable fact. That a "curve of stature" should agree closely with the "normal curve of error" amazed Galton, and (as he said) formed the mainstay of his long and fruitful enquiry into natural inheritance*. The curve is a thing apart, *sui generis*. It depicts no course of events, it is no time or vector diagram. It merely deals with the variability, and variation, of magnitudes; and by magnitudes we mean anything which can be counted or measured, a regiment of men, a basket of

* Stature itself, in a homogeneous population, is a good instance of a normal frequency distribution, save only that the spread or range of variation is unusually low; for one-half of the population of England differs by no more than an inch and a half from the average of them all. Variation is said to be greater among the negroid than among the white races, and it is certainly very great from one race to another: e.g. from the Dinkas of the White Nile with a mean height of 1.8 m. to the Congo pygmies averaging 1.35, or say 5 ft. 11 in. and 4 ft. 6 in. respectively.

nuts, the florets of a daisy, the stripes of a zebra, the nearness of shots to the bull's eye*. It thereby illustrates one of the most far-reaching, some say one of the most fundamental, of nature's laws.

We find the curve of error manifesting itself in the departures from a mean value, which seems itself to be merely accidental—as, for instance, the mean height or weight of ten-year-old English boys; but we find it no less well displayed when a certain definite or normal number is indicated by the nature of the case. For instance the Medusae, or jelly-fishes, have a "radiate symmetry" of eight nodes and internodes. But even so, the number eight is subject to variation, and the instances of more or less group themselves in a Gaussian curve.

*Number of "tentaculocysts" in Medusae (*Ephyra* and *Aurelia*)*

(Data from E. T. Browne, Q.J.M.S. xxxvii, p. 245, 1895)

	5	6	7	8	9	10	11	12	13	14	15
<i>Ephyra</i> (1893)	—	4	8	278	22	18	12	14	3	—	—
" (1894)	1	6	34	883	75	61	35	17	3	1	—
<i>Aurelia</i> (1894)	—	2	18	296	33	16	18	7	—	—	1

Percentage numbers:

<i>Ephyra</i>	—	1·1	2·2	77·4	6·1	5·0	3·3	3·9	0·8	—	—
"	—	0·5	3·0	79·0	6·7	5·4	3·1	1·4	0·2	—	—
<i>Aurelia</i>	—	0·5	4·7	77·2	8·6	4·1	2·6	1·8	—	—	—
Mean	—	0·7	3·3	77·9	7·1	4·8	3·0	2·4	0·3	—	—

The curve of error is a "bell-shaped curve," a *courbe en cloche*. It rises to a maximum, falls away on either side, has neither beginning nor end. It is (normally) symmetrical, for lack of cause to make it otherwise; it falls off faster and then slower the farther it departs from the mean or middle line; it has a "point of inflexion," of necessity on either side, where it changes its curvature and from being concave to the middle line spreads out to become convex

* "I know of scarcely anything (says Galton) so apt to impress the imagination as the wonderful form of cosmic order expressed by the Law of Frequency of Error....It reigns with serenity and in complete self-effacement amidst the wildest confusion" (*Natural Inheritance*, p. 62). Observe that Galton calls it the "law of frequency of error," which is indeed its older and proper name. Cf. (*int. al.*) P. G. Tait, *Trans R.S.E.* xxiv, pp. 139–145, 1867.

thereto. If we pour a bushel of corn out of a sack, the outline or profile of the heap resembles such a curve; and wellnigh every hill and mountain in the world is analogous (even though remotely) to that heap of corn*. Causes beyond our ken have cooperated to place and allocate each grain or pebble; and we call the result a "random distribution," and attribute it to fortuity, or chance. Galton devised a very beautiful experiment, in which a sloping tray is beset with pins, and sand or millet-seed poured in at the top. Every falling grain has its course deflected again and again; the final distribution is emphatically a random one, and the curve of error builds itself up before our eyes.

The curve as defined by Gauss, *princeps mathematicorum*—who in turn was building on Laplace†—is at once empirical and theoretical‡; and Lippmann is said to have remarked to Poincaré: "Les expérimentateurs s'imaginent que c'est un théorème de mathématique, et les mathématiciens d'être un fait expérimental!" It is theoretical in so far as its equation is based on certain hypothetical considerations: viz. (1) that the arithmetic mean of a number of variants is their best or likeliest average, an axiom which is obviously true in simple cases—but not necessarily in all; (2) that "fortuity" implies the absence of any predominant, decisive or overwhelming cause, and connotes rather the coexistence and joint effect of small, undefined but independent causes, many or few:

* If we pour the corn out carefully through a small hole above, the heap becomes a cone, with sides sloping at an "angle of repose"; and the cone of Fujiyama is an exquisite illustration of the same thing. But in these two instances one predominant cause outweighs all the rest, and the distribution is no longer a random one.

† The Gaussian curve of error is really the "second curve of error" of Laplace. Laplace's first curve of error (which has uses of its own) consists of two exponential curves, joining in a sharp peak at the median value. Cf. W. J. Luyten, *Proc. Nat. Acad. Sci.* xviii, pp. 360–365, 1932.

‡ The Gaussian equation to the normal frequency distribution or "curve of error" need not concern us further, but let us state it once for all:

$$y = \frac{1}{\sqrt{2\pi}} e^{-\frac{(x_a-x)^2}{2}},$$

where x_a is the abscissa which gives the maximum ordinate, and where the maximum ordinate, $y_0 = 1/\sqrt{2\pi}$. Thus the log of the ordinate is a quadratic function of the abscissa; and a simple property, fundamental to the curve, is that for equally spaced ordinates (starting anywhere) the square of any ordinate divided by the product of its neighbours gives a scalar quantity which is constant all along (G.T.B.).

producing their several variations, deviations or errors; and potent in their combinations, permutations and interferences*.

We begin to see why bodily dimensions lend, or submit, themselves to this masterful law. Stature is no single, simple thing; it is compounded of bones, cartilages and other elements, variable each in its own way, some lengthening as others shorten, each playing its little part, like a single pin in Galton's toy, towards a "fortuitous" resultant. "The beautiful regularity in the statures of a population (says Galton) whenever they are statistically marshalled in the order of their heights, is due to the number of variable and quasi-independent elements of which stature is the sum." In a bagful of pennies fresh from the Mint each coin is made by the single stroke of an identical die, and no ordinary weights and measures suffice to differentiate them; but in a bagful of old-fashioned hand-made nails a slow succession of repeated operations has drawn the rod and cut the lengths and hammered out head, shaft and point of every single nail—and a curve of error depicts the differences between them.

The law of error was formulated by Gauss for the sake of the astronomers, who aimed at the highest possible accuracy, and strove so to interpret their observations as to eliminate or minimise their inevitable personal and instrumental errors. It had its roots also in the luck of the gaming-table, and in the discovery by eighteenth-century mathematicians that "chance might be defined in terms of mathematical precision, or mathematical 'law'." It was Quetelet who, beginning as astronomer and meteorologist, applied the "law of frequency of error" for the first time to biological statistics, with which in name and origin it had nothing whatsoever to do.

The intrinsic significance of the theory of probabilities and the law of error is hard to understand. It is sometimes said that to forecast the future is the main purpose of statistical study, and *expectation*, or *expectancy*, is a common theme. But all the theory

* "The curve of error would seem to carry the great lesson that the ultimate differences between individuals are simple and few; that they depend on collisions and arrangements, on permutations and combinations, on groupings and interferences, of elementary qualities which are *limited in variety and finite in extent*" (J. M. Keynes). A connection between this law and Mendelian inheritance is discussed by John Brownlee, *P.R.S.E.* xxxi, p. 251, 1910.

in the world enables us to foretell no single unknown thing, not even the turn of a card or the fall of a die. The theory of probabilities is a development of the theory of combinations, and only deals with what occurs, or has occurred, in *the long run*, among large numbers and many permutations thereof. Large numbers simplify many things; a million men are easier to understand than one man out of a million. As David Hume* said: "What depends on a few persons is in a great measure to be ascribed to chance, or to secret and unknown causes; what arises from a great many may often be accounted for by determinate and known causes." Physics is, or has become, a comparatively simple science, just because its laws are based on the statistical averages of innumerable molecular or primordial elements. In that invisible world we are sometimes told that "chance" reigns, and "uncertainty" is the rule; but such phrases as *mere chance*, or *at random*, have no meaning at all except with reference to the knowledge of the observer, and a thing is a "pure matter of chance" when it depends on laws which we do not know, or are not considering†. Ever since its inception the merits and significance of the theory of probabilities have been variously estimated. Some say it touches the very foundations of knowledge‡; and others remind us that "avec les chiffres on peut tout démontrer." It is beyond doubt, it is a matter of common experience, that probability plays its part as a guide to reasoning. It extends, so to speak, the theory of the syllogism, and has been called the "logic of uncertain inference"§.

In measuring a group of natural objects, our measurements are uncertain on the one hand and the objects variable on the other; and our first care is to measure in such a way, and to such a scale, that our own errors are small compared with the natural variations. Then, having made our careful measurements of a group, we want to know more of the *distribution* of the several magnitudes, and

* *Essay XIV.*

† So Leslie Ellis and G. B. Airy, in correspondence with Sir J. D. Forbes; see his *Life*, p. 480.

‡ Cf. Hans Reichenbach, *Les fondements logiques du calcul des probabilités*, *Annales de l'inst. Poincaré*, VII, pp. 267, 1937.

§ Cf. J. M. Keynes, *A Treatise on Probability*, 1921; and A. C. Aitken's *Statistical Mathematics*, 1939.

especially to know two important things. We want a *mean value*, as a substitute for the *true value** if there be such a thing; let us use the arithmetic mean to begin with. About this mean the observed values are grouped like a target hit by skilful or unskilful shots; we want some measure of their inaccuracy, some measure of their *spread*, or *scatter*, or dispersion, and there are more ways than one of measuring and of representing this. We do it visibly and graphically every time we draw the curve (or polygon) of frequency; but we want a means of description or tabulation, in words or in numbers. We find it, according to statistical mathematics, in the so-called *index of variability*, or *standard deviation* (σ), which merely means the average deviation from the mean†. But we must take some precautions in determining this average; for in the nature of things these deviations err both by excess and defect, they are partly positive and partly negative, and their mean value is the mean of the variants themselves. Their squares, however, are all positive, and the mean of these takes account of the magnitude of each deviation with no risk of cancelling out the positive and negative terms: but the "dimension" of this average of the squares is wrong. The square root of this average of squares restores the correct dimension, and the result is the useful index of variability, or of deviation, which is called σ ‡.

This standard deviation divides the area under the normal curve *nearly* into equal halves, and *nearly* coincides with the point of inflexion on either side; it is the simplest algebraic measure of dispersion, as the mean is the simplest arithmetical measure of position. When we divide this value by the mean, we get a figure

* It is not always obvious what the "errors" are, nor what it is that they depart or deviate from. We are apt to think of the arithmetic mean, and to leave it at that. But were we to try to ascertain the ratio of circumference to diameter by measuring pennies or cartwheels, our "errors" would be found grouped round a mean value which no simple arithmetic could define.

† σ , the standard deviation, was chosen for its convenience in mathematical calculation and formulation. It has no special biological significance; and a simpler index, the "inter-quartile distance," has its advantages for the non-mathematician, as we shall see presently.

‡ That is to say: Square the deviation-from-the-mean of each class or ordinate (ξ); multiply each by the number of instances (or "variates") in that class (f); divide by the total number (N); and take the square-root of the whole: $\sigma^2 = \frac{\sum (\xi^2 f)}{N}$.

which is independent of any particular units, and which is called the *coefficient of variability**.

Karl Pearson, measuring the amount of variability in the weight and height of man, found this coefficient to run as follows: In male new-born infants, for weight 15·6, and for stature 6·5; in male adults, for weight 10·8, and for stature 3·6. Here the amount of variability is thrice as great for weight as for stature among grown men, and about $2\frac{1}{2}$ times as great in infancy†. The same curious fact is well brought out in some careful measurements of shell-fish, as follows:

*Variability of young Clams (*Mactra sp.*)‡*

Age (years)	Average size		Coefficient of variability	
	1	2	1	2
Number in sample	41	20	41	20
Length (cm.)	3·2	6·3	15·3	6·3
Height	2·3	4·7	14·0	6·7
Thickness	1·3	2·8	9·6	8·3
Weight (gm.)	6·4	59·8	35·4	18·5

The phenomenon is purely mathematical. Weight varies as the product of length, height and depth, or (as we have so often seen) as the cube of any one of these dimensions in the case of similar figures. It is then a mathematical, rather than a biological fact that, for small deviations, the variability of the whole tends to be equal to the *sum* of that of the three constituent dimensions. For if weight, w , varies as height x , breadth y , and depth z , we may write

$$w = c \cdot xyz.$$

Whence, differentiating, $\frac{dw}{w} = \frac{dx}{x} + \frac{dy}{y} + \frac{dz}{z}$.

We see that among the shell-fish there is much more variability in the younger than in the older brood. This may be due to

* It is usually multiplied by 100, to make it of a handier amount; and we may then define this coefficient, C , as $= \sigma/M \times 100$.

† Cf. Fr. Boas, Growth of Toronto children, *Rep. of U.S. Comm. of Education*, 1896–7, 1898, pp. 1541–1599; Boas and Clark Wissler, Statistics of growth, *Education Rep.* 1904, 1906, pp. 25–132; H. P. Bowditch, *Rep. Mass. State Board of Health*, 1877; K. Pearson, On the magnitude of certain coefficients of correlation in man, *Proc. R.S.* LXVI, 1900; S. Nagai, Körperkonstitution der Japaner, from Brugsch-Levy, *Biologie d. Person.* II, p. 445, 1928; R. M. Fleming, A study of growth and development, *Medical Research Council, Special Report*, No. 190, 1933.

‡ From F. W. Weymouth, *California Fish Bulletin*, No. 7, 1923.

inequality of age; for in a population only a few weeks old, a few days sooner or later in the date of birth would make more difference than later on. But a more important matter, to be seen in mankind (Fig. 22), is that variability of stature runs *pari passu*, or nearly so, with the rate of growth, or curve of annual increments (cf. Fig. 12). The curve of variability descends when the growth-rate slackens, and rises high when in late boyhood growth is speeded up. In short, the amount of variability in stature or in weight is correlated with, or is a function of, the rate of growth in these magnitudes.

Judging from the evidence at hand, we may say that variability reaches its height in man about the age of thirteen or fourteen, rather earlier in the girls than in the boys, and rather earlier in the case of stature than of weight. The difference in this respect between the boys and the girls is now on one side, now on the other. In infancy variability is greater in the girls; the boys shew it the more at five or six years old; about ten years old the girls have it again. From twelve to sixteen the boys are much the more variable, but by seventeen the balance has swung the other way (Fig. 23).

Coefficient of variability ($\sigma/M \times 100$) in man, at various ages

Age	...	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Stature															
British (Fleming):															
Boys	5.1	5.4	5.0	5.3	5.4	5.6	5.7	5.6	5.8	5.8	5.8	5.0	4.3	3.0	
Girls	5.2	5.2	5.0	5.5	5.4	5.6	5.8	5.7	5.6	4.7	4.2	3.9	3.7	3.8	
American (Bowditch)	4.8	4.6	4.4	4.5	4.4	4.6	4.7	4.9	5.5	5.8	5.6	5.5	4.6	3.7	3.7
Japanese (Nagai):															
Boys	—	4.0	—	4.3	—	4.1	—	4.0	5.0	5.0	4.2	3.2	—	—	—
Girls	—	4.3	—	4.1	—	4.5	—	4.5	4.6	3.6	3.1	3.0	—	—	—
Mean	—	4.7	—	4.7	—	4.9	—	5.0	5.3	5.0	4.6	4.1	—	—	—
Weight															
American	11.6	10.3	11.1	9.9	11.0	1.6	1.8	13.7	3.6	6.8	15.3	13.3	13.0	10.4	
Japanese:	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Boys	—	10.3	—	12.1	—	0.8	—	7.0	5.1	7.0	13.8	10.9	—	—	—
Girls	—	10.2	—	11.2	—	2.1	—	15.0	5.6	3.4	11.4	11.5	—	—	—
Mean	—	10.3	—	11.1	—	11.5	—	11.9	14.8	15.7	13.5	11.9	—	—	—

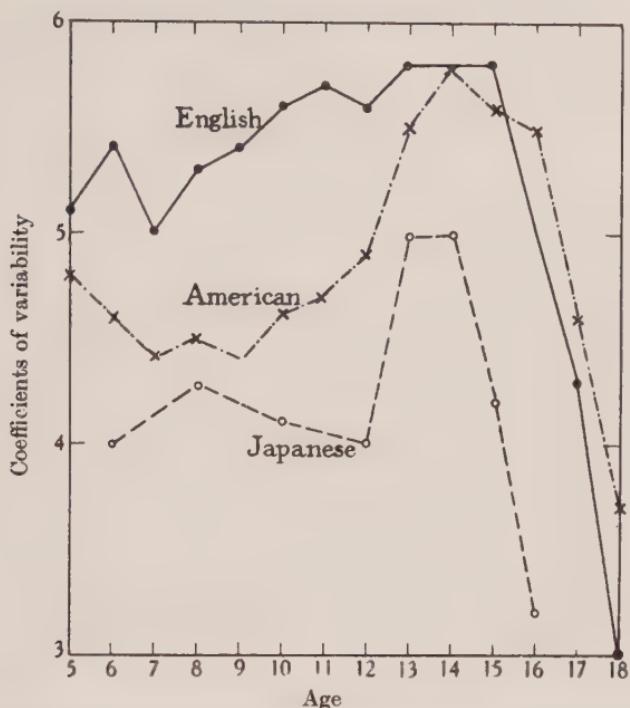


Fig. 22. Variability in stature (boys). After Fleming, Bowditch and Nagai.

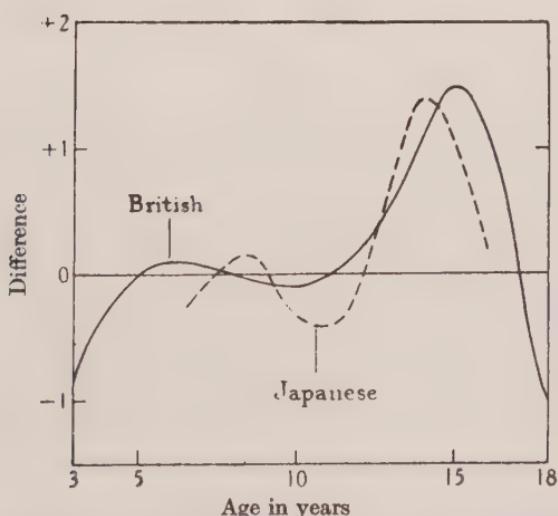


Fig. 23. Coefficient of variability in stature: excess or defect of this coefficient in the boy over the girl. Data from R. M. Fleming, and from Nagai.

The amount of variability is bound to differ from one race or nationality to another, and we find big differences between the Americans and the Japanese, both in magnitude and phase (Fig. 22).

If we take not merely the variability of stature or weight at a given age, but the variability of the yearly *increments*, we find that this latter variability tends to increase steadily, and more and more rapidly, within the ages for which we have information; and this phenomenon is, in the main, easy of explanation. For a great part of the difference between one individual and another in regard to rate of growth is a mere difference of *phase*—a difference in the epochs of acceleration and retardation, and finally a difference as to the epoch when growth comes to an end; it follows that variability will be more and more marked as we approach and reach the period when some individuals still continue, and others have already ceased, to grow. In the following epitomised table, I have taken Boas's determinations* of the standard deviation (σ), converted them into the corresponding coefficients of variability ($\sigma/M \times 100$), and then smoothed the resulting numbers:

Coefficients of variability in annual increments of stature

Age ...	7	8	9	10	11	12	13	14	15
Boys	17.3	15.8	18.6	19.1	21.0	24.7	29.0	36.2	46.1
Girls	17.1	17.8	19.2	22.7	25.9	29.3	37.0	44.8	—

The greater variability in the girls is very marked †, and is explained (in part at least) by the more rapid rate at which the girls run through the several phases of their growth (Fig. 24). To say that children of a given age vary in the rate at which they are growing would seem to be a more fundamental statement than that they vary in the size to which they have grown.

Just as there is a marked difference in phase between the growth-curves of the two sexes, that is to say a difference in the epochs when growth is rapid or the reverse, so also, within each sex, will there be room for similar, but individual, phase-differences. Thus we may have children of accelerated development, who at a given

* *Op. cit.* p. 1548.

† That women are on the whole more variable than men was argued by Karl Pearson in one of his earlier essays: *The Chances of Death and other Studies*, 1897.

epoch after birth are growing rapidly and are already "big for their age"; and others, of retarded development, who are comparatively small and have not reached the period of acceleration which, in greater or less degree, will come to them in turn. In other words, there must under such circumstances be a strong positive "coefficient of correlation" between stature and rate of growth, and also between

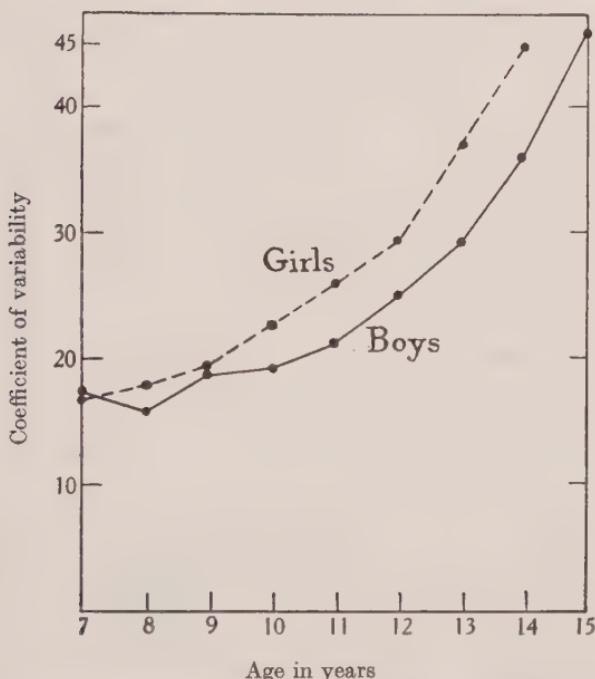


Fig. 24. Coefficients of variability, in annual increments of stature.
After Boas.

the rate of growth in one year and the next. But it does not by any means follow that a child who is precociously big will continue to grow rapidly, and become a man or woman of exceptional stature *. On the contrary, when in the case of the precocious or "accelerated" children growth has begun to slow down, the back-

* Some first attempts at analysis seem to shew that the size of the embryo at birth, or of the seed at germination, has more influence than we were wont to suppose on the ultimate size of plant or animal. See (e.g.) Eric Ashby, Heterosis and the inheritance of acquired characters, *Proc. R.S. (B)*, No. 833, pp. 431-441, 1937; and papers quoted therein.

ward ones may still be growing rapidly, and so making up (more or less completely) on the others. In other words, the period of high positive correlation between stature and increment will tend to be followed by one of negative correlation. This interesting and important point, due to Boas and Wissler*, is confirmed by the following table:

*Correlation of stature and increment in boys and girls
(From Boas and Wissler)*

Age 6	7	8	9	10	11	12	13	14	15
Stature (B)	112.7	115.5	123.2	127.4	133.2	136.8	142.7	147.3	155.9	162.2
(G)	111.4	117.7	121.4	127.9	131.8	136.7	144.6	149.7	153.8	157.2
Increment (B)	5.7	5.3	4.9	5.1	5.0	4.7	5.9	7.5	6.2	5.2
(G)	5.9	5.5	5.5	5.9	6.2	7.2	6.5	5.4	3.3	1.7
Correlation (B)	0.25	0.11	0.08	0.25	0.18	0.18	0.48	0.29	-0.42	-0.44
(G)	0.44	0.14	0.24	0.47	0.18	-0.18	-0.42	-0.39	-0.63	0.11

A minor but very curious point brought out by the same investigators is that, if instead of stature we deal with height in the sitting posture (or, practically speaking, with length of trunk or back), then the correlations between this height and its annual increment are throughout negative. In other words, there would seem to be a general tendency for the long trunks to grow slowly throughout the whole period under investigation. It is a well-known anatomical fact that tallness is in the main due not to length of body but to length of limb.

Since growth in height and growth in weight have each their own velocities, and these fluctuate, and even the amount of their variability alters with age, it follows that the *correlation* between height and weight must not only also vary but must tend to fluctuate in a somewhat complicated way. The fact is, this correlation passes through alternate maxima and minima, chief among which are a maximum at about fourteen years of age and a minimum about twenty-one. Other intercorrelations, such as those between height or weight and chest-measurement, shew their periodic variations in like manner; and it is about the time of puberty

* *I.c.* p. 42, and other papers there quoted. Cf. also T. B. Robertson, *Criteria of Normality in the Growth of Children*, Sydney, 1922.

that correlation tends to be closest, or a *norm* to be most nearly approached*.

The whole subject of variability, both of magnitude and rate of increment, is highly suggestive and instructive: inasmuch as it helps further to impress upon us that growth and specific *rate of growth* are the main physiological factors, of which specific magnitude, dimensions and form are the concrete and visible resultant. Nor may we forget for a moment that growth-rate, and growth itself, are both of them very complex things. The increase of the active tissues, the building of the skeleton and the laying up of fat and other stores, all these and more enter into the complex phenomenon of growth. In the first instance we may treat these many factors as though they were all one. But the breeder, and the geneticist will soon want to deal with them apart; and the mathematician will scarce look for a simple expression where so many factors are involved. But the problems of variability, though they are intimately related to the general problem of growth, carry us very soon beyond our limitations.

The curve of error

To return to the curve of error.

The normal curve is a symmetrical one. Its middle point, or *median ordinate*, marks the arithmetic *mean* of all the measurements; it is also the *mode*, or class to which the largest number of individual instances belong. *Mean*, *median* and *mode* are three different sorts of average; but they are one and the same in the normal curve.

It is easy to produce a related curve which is not symmetrical, and in which mean, median and mode are no longer the same. The heap of corn will be lop-sided or "skew" if the wind be blowing while the grain is falling: in other words, if some prevailing cause disturb the quasi-equilibrium of fortuity; and there are other ways, some simple, some more subtle, by which asymmetry may be impressed upon our curve.

The Gaussian curve is only one of many similar bell-shaped curves; and the binomial coefficients, the numerical coefficients of $(a + b)^n$, yield a curve so like it that we may treat them as the same. The

* Cf. Joseph Bergson, Growth-changes in physical correlation, *Human Biology*, I, p. 4, 1930.

Gaussian curve extends, in theory, to infinity at either end; and this infinite extension, or asymptotism, has its biological significance. We know that this or that athletic record is lowered, slowly but continually, as the years go by. This is due in part, doubtless, to increasing skill and improved technique; but quite apart from these the record would slowly fall as more and more races are run, owing to the indefinite extension of the Gaussian curve*.

On the other hand, while the Gaussian curve extends in theory to infinity, the fact that variation is always limited and that *extreme* variations are infinitely rare is one of the chief lessons of the law of frequency. If, in a population of 100,000 men, 170 cm. be the mean height and 6 cm. the standard deviation, only 11 per cent., or say 130 men, will exceed 188 cm., only 10 men will be over 191 cm., and only one over 193 cm., or $13\frac{1}{2}$ per cent. above the average. The chance is negligible of a single one being found over 210 cm., or 7 ft. high, or 24 per cent. above the average.

Yet, widely as the law holds good, it is hardly safe to count it as a universal law. Old Parr at 150 years old, or the giant Chang at more than eight feet high, are not so much extreme instances of a law of probability, as exceptional cases due to some peculiar cause or influence coming in†. In a somewhat analogous way, one or two species in a group grow far beyond the average size; the Atlas moth, the Goliath beetle, the ostrich and the elephant, are far-off outliers from the groups to which they belong. A reason is not easy to find. It looks as though variations came at last to be in proportion to the size attained, and so to go on by compound interest or geometrical progression. There may be nothing surprising in this; nevertheless, it is in contradistinction to that summation of small fortuitous differences which lies at the root of the law of error. If size vary in proportion to the magnitude of the variant individuals, not only

* This is true up to a certain extent, but would become a mathematical fiction later on. There will be physical limitations (as there are in quantum mechanics) both to record-breaking, and to the measurement of minute extensions of the record.

† We may indeed treat old Parr's case on the ordinary lines of actuarial probability, but it is "without much actuarial importance." The chance of his record being broken by a modern centenarian is reckoned at $(\frac{1}{2})^{50}$, by Major Greenwood and J. C. Irwin, writing on Senility, in *Human Biology*, xi, pp. 1-23, 1939.

will the frequency curve be obviously skew, but the *geometric mean*, not the arithmetic, becomes the most probable value*. Now the logarithm of the geometric mean of a series of numbers is the arithmetic mean of their logarithms; and it follows that in such cases the logarithms of the variants, and not the variants themselves, will tend to obey the Gaussian law and follow the normal curve of frequency†.

The Gaussian curve, and the standard deviation associated with it, were (as we have seen) invented by a mathematician for the use

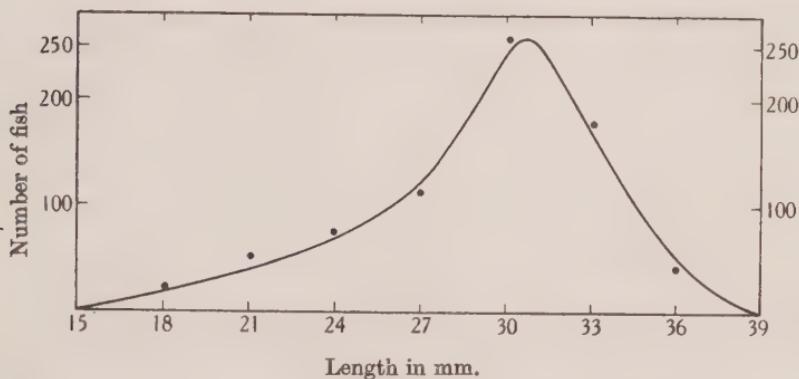


Fig. 25 A. Curve of frequency of a population of minnows.

of an astronomer, and their use in biology has its difficulties and disadvantages. We may do much in a simpler way. Choosing a random example, I take a catch of minnows, measured in 3 mm. groups, as follows (Fig. 25A):

Size (mm.)	13-15	16-18	19-21	22-24	25-27	28-30	31-33	34-36	37-39
Number	1	22	52	67	114	257	177	41	2

* See especially J. C. Kapteyn, Skew frequency curves in biology and statistics, *Rec. des Trav. Botan. Néerland.*, Groningen, XIII, pp. 105-158, 1916. Also Axel M. Hemmingsen, Statistical analysis of the differences in body-size of related species, *Danske Vidensk. Selsk. Medd.* xcvi, pp. 125-160, 1934.

† This often holds good. Wealth breeds wealth, hence the distribution of wealth follows a skew curve; but logarithmically this curve becomes a normal one. Weber's law, in physiology, is a well-known instance; on the thresholds of sensations, effects are produced proportional to the magnitudes of those thresholds, and the logs of the thresholds, and not the thresholds themselves, are normally distributed.

Let us sum the same figures up, so as to show the whole number above or below the respective sizes.

Size (mm.)	15	18	21	24	27	30	33	36	39
Number below	1	23	75	142	256	513	690	731	733
Percentage	—	3·1	10·2	19·4	34·9	70·0	94·1	99·6	100

Our first set of figures, the actual measurements, would give us the "courbe en cloche," in the form of an unsymmetrical (or "skew") Gaussian curve: one, that is to say, with a long sloping *talus* on

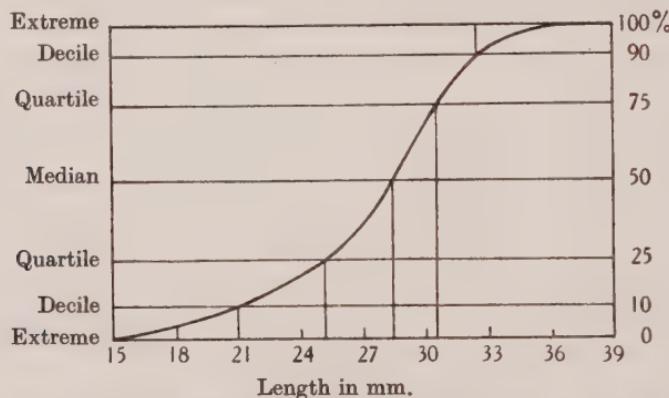


Fig. 25 B. "Curve of distribution" of a population of minnows.

one side of the hill. The other gives us an "**S-shaped curve**," apparently limited, but really asymptotic at both ends (Fig. 25 B); and this **S-shaped curve** is so easy to work with that we may at once divide it into two halves (so finding the "median" value), or into quarters and tenths (giving the "quartiles" and "deciles"), or as we please. In short, after drawing the curve to a larger scale, we shall find that we can safely read it to thirds of a millimetre, and so draw from it the following somewhat rough but very useful tabular epitome of our population of minnows, from which the curve can be reconstructed at any time:

	mm.
Extreme	13
First decile	21·0
Lower quartile	25·3
<i>Median</i>	28·6
Upper quartile	30·6
Last decile	32·3
Extreme	39

This S-shaped "summation-curve" is what Francis Galton called a *curve of distribution*, and he "liked it the better the more he used it." The spread or "scatter" is conveniently and immediately estimated by the distance between the two quartiles; and it happens that this *very nearly coincides* with the standard deviation of the normal curve.

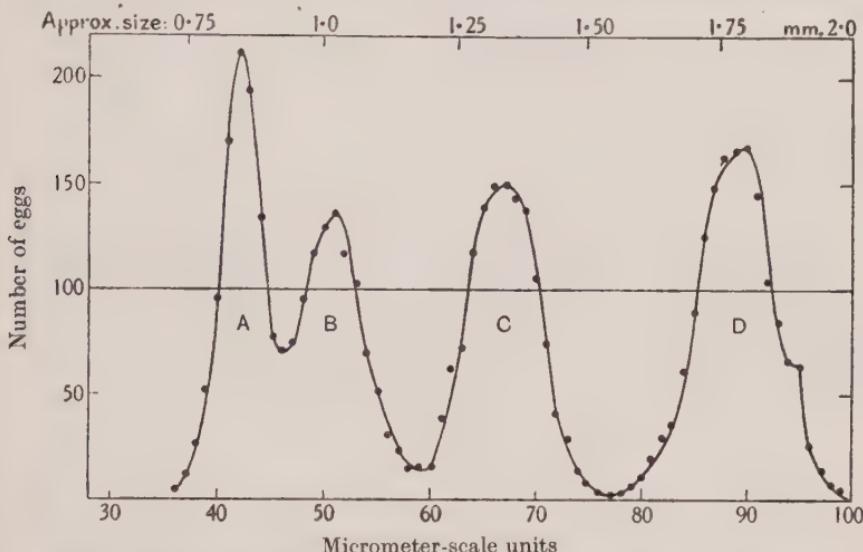


Fig. 26. A plankton-sample of fish-eggs: North of Scotland, February 1905.
(Only eggs without oil-globule are counted here.)

A. Dab and Flounder. B, *Gadus Esmarckii* and *G. luscus*.
C, Cod and Haddock. D, Plaice.

There are biological questions for which we want all the accuracy which biometric science can give; but there are many others on which such refinements are thrown away.

Mathematically speaking, we cannot integrate the Gaussian curve, save by using an infinite series; but to all intents and purposes we are doing so, graphically and very easily, in the illustration we have just shewn. In any case, whatever may be the precise character of each, we begin to see how our two simplest curves of growth, the bell-shaped and the S-shaped curve, form a reciprocal pair, *the integral and the differential of one another**—like the distance travelled

* It is of considerable historical interest to know that this *practical* method of summation was first used by Edward Wright, in a Table of Latitudes published in his *Certain Errors in Navigation corrected*, 1599, as a means of virtually integrating $\sec x$. (On this, and on Wright's claim to be the inventor of logarithms, see Florian Cajori, in *Napier Memorial Volume*, 1915, pp. 94–99.)

and the velocity of a moving body. If $y = e^{-x^2}$ be the ordinate of the one, $z = \int e^{-x^2} dx$ is that of the other.

There is one more kind of frequency-curve which we must take passing note of. We begin by thinking of our curve, whether symmetrical or skew, as the outcome of a single homogeneous group. But if we happen to have two distinct but intermingled groups to deal with, differing by ever so little in kind, age, place or circumstance—leaves of both oak and beech, heights of both men and women—this heterogeneity will tend to manifest itself in two separate cusps, or modes, on the common curve: which is then indeed two curves rolled into one, each keeping something of its own individuality. For example, the floating eggs of the food-fishes are much alike, but differ appreciably in size. A random gathering, netted at the surface of the sea, will yield on measurement a multi-modal curve, each cusp of which is recognisable, more or less certainly, as belonging to a particular kind of fish (Fig. 26).

A further note upon curves

A statistical “curve”, such as Quetelet seems to have been the first to use*, is a device whose peculiar and varied beauty we are apt, through familiarity, to disregard. The curve of frequency which we have been studying depicts (as a rule) the distribution of magnitudes in a material system (a population, for instance) at a certain epoch of time; it represents a given *state*, and we may call it a *diagram of configuration*†. But we oftener use our curves to compare successive states, or changes of magnitude, as one configuration gives place to another; and such a curve may be called a *diagram of displacement*. An imaginary point moves in imaginary space, the dimensions of which represent those of the phenomenon in question, dimensions which we may further define and measure by a system of “coordinates”; the movements of our point through its figurative space are thus analogous to, and illustrative of, the events which constitute the phenomenon. Time is often represented, and measured, on one of the coordinate axes, and our diagram of “displacement” then becomes a *diagram of velocity*.

* In his *Théorie des probabilités*, 1846.

† See Clerk Maxwell's article “Diagrams,” in the *Encyclopaedia Britannica*, 9th edition.

This simple method (said Kelvin) of shewing to the eye the law of variation, however complicated, of an independent variable, is one of the most beautiful results of mathematics*.

We make and use our curves in various ways. We set down on the coordinate network of our chart the points given by a series of observations, and connect them up into a continuous series as we chart the voyage of a ship from her positions day by day; we may "smooth" the line, if we so desire. Sometimes we find our points so crowded, or otherwise so dispersed and distributed, that a line can be drawn not from one to another but *among them all*—a method first used by Sir John Herschel†, when he studied the orbits of the double stars. His delicate observations were affected by errors, at first sight without rhyme or reason, but a curve drawn where the points lay thickest embodied the common lesson of them all; any one pair of observations would have sufficed, whether better or worse, for the calculation of an orbit, but Herschel's dot-diagram obtained "from the whole assemblage of observations taken together, and regarded as a single set of data, a single result in whose favour they all conspire." It put us in possession, said Herschel, of something truer than the observations themselves‡; and Whewell remarked that it enabled us to obtain laws of Nature not only from good but from very imperfect observations§. These are some advantages of the use of "curves," which have made them essential to research and discovery.

It is often helpful and sometimes necessary to *smooth* our curves,

* Kelvin, *Nature*, xxix, p. 440, 1884.

† *Mem. Astron. Soc.* v, p. 171, 1830; *Nautical Almanack*, 1835, p. 495; etc.

‡ Here a certain distinction may be observed. We take the average height of a regiment, because the men actually vary about a mean. But in estimating the place of a star, or the height of Mont Blanc, we average *results* which only differ by personal or instrumental error. It is this latter process of averaging which leads, in Herschel's phrase, to results more trustworthy than observation itself. Laplace had made a similar remark long before (*Oeuvres*, vii, *Théorie des probabilités*): that we may ascertain the very small effect of a constant cause, by means of a long series of observations the errors of which exceed the effect itself. He instances the small deviation to the eastward which the rotation of the earth imposes on a falling body. In like manner the mean level of the sea may be determined to the second decimal of an inch by observations of high and low water taken roughly to the nearest inch, provided these are faithfully carried out at every tide, for say a hundred years. Cf. my paper on Mean Sea Level, in *Scottish Fishery Board's Sci. Report* for 1915.

§ *Novum Organum Renovatum* (3rd ed.), 1858, p. 20.

whether at free hand or by help of mathematical rules; it is one way of getting rid of non-essentials—and to do so has been called the very key-note of mathematics*. A simple rule, first used by Gauss, is to replace each point by a mean between it and its two or more neighbours, and so to take a “floating” or “running average.” In so doing we trade once more on the “principle of continuity”; and recognise that in a series of observations each one is related to another, and is part of the contributory evidence on which our knowledge of all the rest depends. But all the while we feel that Gaussian smoothing gives us a practical or descriptive result, rather than a mathematical one.

Some curves are more elegant than others. We may have to rest content with points in which no order is apparent, as when we plot the daily rainfall for a month or two; for this phenomenon is one whose regularity only becomes apparent over long periods, when average values lead at last to “statistical uniformity.” But the most irregular of curves may be instructive if it coincide with another not less irregular: as when the curve of a nation’s birth-rate, in its ups and downs, follows or seems to follow the price of wheat or the spots upon the sun.

It seldom happens, outside of the exact sciences, that we comprehend the mathematical aspect of a phenomenon enough to *define* (by formulae and constants) the curve which illustrates it. But, failing such thorough comprehension, we can at least speak of the *trend* of our curves and put into words the character and the course of the phenomena they indicate. We see how this curve or that indicates a uniform velocity, a tendency towards acceleration or retardation, a periodic or non-periodic fluctuation, a start from or an approach to a limit. When the curve becomes, or approximates to, a mathematical one, the types are few to which it is likely to belong†. A straight line, a parabola, or hyperbola, an exponential or a logarithmic curve (like $x = ay^b$), a sine-curve or sinusoid, damped or no, suffice for a wide range of phenomena; we merely modify our scale, and change the names of our coordinates.

* Cf. W. H. Young, The mathematic method and its limitations, *Atti del Congresso dei Matematici, Bologna, 1928*, I, p. 203.

† Hence the engineer usually begins, for his first tentative construction, by drawing one of the familiar curves, catenary, parabola, arc of a circle, or curve of sines.

The curves we mostly use, other than the Gaussian curve, are *time-diagrams*. Each has a beginning and an end; and one and the same curve may illustrate the life of a man, the economic history of a kingdom, the schedule of a train between one station and another. What it then shews is a velocity, an acceleration, and a subsequent negative acceleration or retardation. It depicts a "mechanism" at work, and helps us to see analogous mechanisms in different fields; for Nature rings her many changes on a few simple themes. The same expressions serve for different orders of phenomena. The swing of a pendulum, the flow of a current, the attraction of a magnet, the shock of a blow, have their analogues in a fluctuation of trade, a wave of prosperity, a blow to credit, a tide in the affairs of men.

The same exponential curve may illustrate a rate of cooling, a loss of electric charge, the chemical action of a ferment or a catalyst. The S-shaped population-curve or "logistic curve" of Verhulst (to which we are soon coming) is the hysteresis-curve by which Ewing represented self-induction in a magnetic field; it is akin to the path of a falling body under the influence of friction; and Lotka has drawn a curve of the growing mileage of American railways, and found it to be a typical logistic curve. A few bars of music plotted in wave-lengths of the notes might be mistaken for a tidal record. The periodicity of a wave, the acceleration of gravity, retardation by friction, the role of inertia, the explosive action of a spark or an electric contact—these are some of the modes of action or "forms of mechanism" which recur in limited number, but in endless shapes and circumstances*. The way in which one curve fits many phenomena is characteristic of mathematics itself, which does not deal with the specific or individual case, but *generalises* all the while, and is fond (as Henri Poincaré said) of giving the same name to different things.

Our curves, as we have said, are mostly time-diagrams, and represent a change in time from one magnitude to another; they are diagrams of displacement, in Maxwell's phrase. We may consider four different cases, not equally simple mathematically, but all

* See an admirable little book by Michael Petrovich, *Les mécanismes communs aux phénomènes disparates*, Paris, 1921.

capable of explanation, up to a certain point, without mathematics.

(1) If in our coordinate diagram we have merely to pass from one isolated *point* to another, a *straight line* joining the two points is the shortest—and the likeliest way.

(2) To rise and fall alternately, going to and fro from maximum to minimum, a zig-zag rectilinear path would still be, geometrically, the shortest way; but it would be sharply discontinuous at every turn, it would run counter to the “principle of continuity,” it is not likely to be nature’s way. A wavy course, with no more change of curvature than is absolutely necessary, is the path which nature follows. We call it a *simple harmonic motion*, and the simplest of

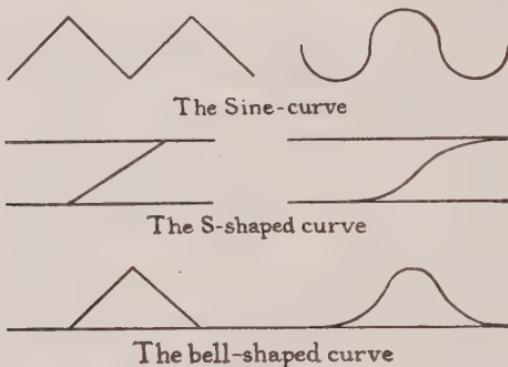


Fig. 27. Simple curves, representing a change from one magnitude to another.

all such wavy curves we call a *sine-curve*. If there be but one maximum and one minimum, which our variant alternates between, the vector pathway may be translated into *polar coordinates*; the vector does what the hands of the clock do, and a *circle* takes the place of the sine-curve.

(3) To pass from a zero-line to a maximum once for all is a very different thing; for now minimum and maximum are both of them continuous states, and the principle of continuity will cause our vector-variant to leave the one gradually, and arrive gradually at the other. The problem is how to go uphill from one level road to another, with the least possible interruption or discontinuity. The path follows an **S**-shaped course; it has an *inflection* midway; and the first phase and the last are represented by horizontal asymptotes. This is an important curve, and a common one. It so far resembles

an "elastic curve" (though it is not mathematically identical with it) that it may be roughly simulated by a watchspring, lying between two parallel straight lines and touching both of them. It has its kinetic analogue in the motion of a pendulum, which starts from rest and comes to rest again, after passing midway through its maximal velocity. It indicates a balance between production and waste, between growth and decay: an approach on either side to a state of rest and equilibrium. It shows the speed of a train between two stations; it illustrates the growth of a simple organism, or even of a population of men. A certain simple and symmetrical case is called the *Verhulst-Pearl curve*, or the *logistic curve*.

(4) Lastly, in order to leave a certain minimum, or zero-line, and return to it again, the simplest way will be by a curve asymptotic to the base-line at both ends—or rather in both directions; it will be a bell-shaped curve, having a maximum midway, and of necessity a point of inflection on either side; it is akin to, and under certain precise conditions it becomes, the *curve of error* or *Gaussian curve*.

Besides the ordinary curve of growth, which is a summation-curve, and the curve of growth-rates, which is its derivative, there are yet others which we may employ. One of these was introduced by Minot*, from a feeling that the rate of growth, or the amount of increment, ought in some way to be equated with the growing structure. Minot's method is to deal, not with the actual increments added in successive periods, but with these successive increments represented as percentages of the amount already reached. For instance, taking Quetelet's values for the height (in centimetres) of a male infant, we have as follows:

Years	0	1	2	3	4
cm.	50.0	69.8	79.1	86.4	92.7

But Minot would state the percentage-growth in each of these four annual periods at 39.6, 13.3, 9.2 and 7.3 per cent. respectively:

Years	0	1	2	3	4
Height (cm.)			50.0	69.8	79.1	86.4	92.7
Increments (cm.)			—	19.8	9.3	7.3	6.3
" (per cent.)			—	39.6	13.3	9.2	7.3

* C. S. Minot, On certain phenomena of growing old, *Proc. Amer. Assoc.* XXXIX, 1890, 21 pp.; Senescence and rejuvenation, *Journ. Physiol.* XII, pp. 97–153, 1891; etc. Criticised by S. Brody and J. Needham, *op. cit.* pp. 401 seq.

Now, in our first curve of growth we plotted length against time, a very simple thing to do. When we differentiate L with respect to T , we have dL/dT , which is rate or velocity, again a very simple thing; and from this, by a second differentiation, we obtain, if necessary, d^2L/dT^2 , that is to say, the acceleration.

But when you take percentages of y , you are determining dy/y , and when you plot this against dx , you have

$$\frac{dy/y}{dx}, \text{ or } \frac{dy}{y \cdot dx}, \text{ or } \frac{1}{y} \cdot \frac{dy}{dx}.$$

That is to say, you are multiplying the thing whose variations you are studying by another quantity which is itself continually varying; and are dealing with something more complex than the original factors*. Minot's method deals with a perfectly legitimate function of x and y , and is tantamount to plotting $\log y$ against x , that is to say, the logarithm of the increment against the time. This would be all to the good if it led to some simple result, a straight line for instance; but it is seldom if ever, as it seems to me, that it does anything of the kind. It has also been pointed out as a grave fault in his method that, whereas growth is a continuous process, Minot chooses an arbitrary time-interval as his basis of comparison, and uses the same interval in all stages of development. There is little use in comparing the percentage increase *per week* of a week-old chick, with that of the same bird at six months old or at six years.

The growth of a population

After dealing with Man's growth and stature, Quetelet turned to the analogous problem of the growth of a population—all the more analogous in our eyes since we know man himself to be a “statistical unit,” an assemblage of organs, a population of cells. He had read

* Schmalhausen, among others, uses the same measure of rate of growth, in the form

$$C_v = \frac{\log V - \log V}{k(t-t)} \rightarrow \frac{dv}{dt} - \frac{1}{v};$$

Malthus's *Essay on Population** in a French translation, and was impressed like all the world by the importance of the theme. He saw that poverty and misery ensue when a population outgrows its means of support, and believed that multiplication is checked both by lack of food and fear of poverty. He knew that there were, and *must be*, obstacles of one kind or another to the unrestricted increase of a population; and he knew the more subtle fact that a population, after growing to a certain height, oscillates about an unstable level of equilibrium†.

Malthus had said that a population grows by geometrical progression (as 1, 2, 4, 8) while its means of subsistence tend rather to grow by arithmetical (as 1, 2, 3, 4)—that one adds up while the other multiplies‡. A geometrical progression is a natural and a

* T. R. Malthus, *An Essay on the Principle of Population, as it affects the Future Improvement of Society, etc.*, 1798 (6th ed. 1826; transl. by P. and G. Prévost, Geneva, 1830, 1845). Among the books to which Malthus was most indebted was *A Dissertation on the Numbers of Mankind in ancient and modern Times*, published anonymously in Edinburgh in 1753, but known to be by Robert Wallace and read by him some years before to the Philosophical Society at Edinburgh. In this remarkable work the writer says (after the manner of Malthus) that mankind naturally increase by successive doubling, and tend to do so thrice in a hundred years. He explains, on the other hand, that "mankind do not actually propagate according to the rule in our tables, or any other constant rule; yet tables of this nature are not entirely useless, but may serve to shew, how much the increase of mankind is prevented by the various causes which confine their number within such narrow limits." Malthus was also indebted to David Hume's *Political Discourse, Of the Populousness of ancient Nations*, 1752, a work criticised by Wallace. See also McCulloch's notes to Adam Smith's *Wealth of Nations*, 1828.

† That the nearest approach to equilibrium in a population is long-continued ebb and flow, a mean level and a tide, was known to Herbert Spencer, and was stated mathematically long afterwards by Vito Volterra. See also Spencer's *First Principles*, ch. 22, sect. 173: "Every species of plant or animal is perpetually undergoing a rhythmical variation in number—now from abundance of food and absence of enemies rising above its average, and then by a consequent scarcity of food and abundance of enemies being depressed below its average.... Amid these oscillations produced by their conflict, lies that average number of the species at which its expansive tendency is in equilibrium with surrounding repressive tendencies." Cf. A. J. Lotka, Analytical note on certain rhythmic relations in organic systems, *Proc. Nat. Acad. Sci.* vi, pp. 410–415, 1920; but cf. also his *Elements of Physical Biology*, 1915, p. 90. An analogy, and perhaps a close one, may be found on the Bourse or money market.

‡ That a population will soon outrun its means of subsistence was a natural assumption in Malthus's day, and in his own thickly populated land. The danger may be postponed and the assumption apparently falsified, as by an Argentine cattle-ranch or prairie wheat-farm—but only so long as we enjoy world-wide freedom of import and exchange.

common thing, and, apart from the free growth of a population or an organism, we find it in many biological phenomena. An epidemic declines, or tends to decline, at a rate corresponding to a geometrical progression; the mortality from zymotic diseases declines in geometrical progression among children from one to ten years old; and the chances of death increase in geometrical progression after a certain time of life for us all*.

But in the ascending scale, the story of the horseshoe nails tells us how formidable a thing successive multiplication becomes†. English law forbids the protracted accumulation of compound interest; and likewise Nature deals after her own fashion with the case, and provides her automatic remedies. A fungus is growing on an oaktree—it sheds more spores in a night than the tree drops acorns in a hundred years. A certain bacillus grows up and multiplies by two in two hours' time; its descendants, did they all survive, would number four thousand in a day, as a man's might in three hundred years. A codfish lays a million eggs and more—all in order that *one pair* may survive to take their parents' places in the world. On the other hand, the humming-birds lay only two eggs, the auks and guillemots only one; yet the former are multitudinous in their haunts, and some say that the Arctic auks and auklets outnumber all other birds in the world. Linnaeus‡ shewed that an annual plant would have a million offspring in twenty years, if only two seeds grew up to maturity in a year.

But multiply as they will, these vast populations have their limits. They reach the end of their tether, the pace slows down, and at last they increase no more. Their world is fully peopled, whether it be an island with its swarms of humming-birds, a test-tube with its myriads of yeast-cells, or a continent with its millions of mankind. Growth, whether of a population or an individual, draws to its natural end; and Quetelet compares it, by a bold metaphor, to the motion of a body in a resistant medium. A typical population grows slowly from an asymptotic minimum; it multiplies quickly;

* According to the Law of Gompertz; cf. John Brownlee, in *Proc. R.S.E.* xxxi, pp. 627–634, 1911.

† Herbert Spencer, A theory of population deduced from the general law of animal fertility, *Westminster Review*, April 1852.

‡ In his essay *De Tellure*, 1740.

it draws slowly to an ill-defined and asymptotic maximum. The two ends of the population-curve define, in a general way, the whole curve between; for so beginning and so ending the curve must pass through a point of inflection, it *must be* an S-shaped curve. It is just such a curve as we have seen under simple conditions of growth in an individual organism.

This general and all but obvious trend of a population-curve has been recognised, with more or less precision, by many writers. It is implicit in Quetelet's own words, as follows: "Quand une population peut se développer librement et sans obstacles, elle croît selon une progression géométrique; si le développement a lieu au milieu d'obstacles de toute espèce qui tendent à l'arrêter, et qui agissent d'une manière uniforme, c'est à dire si l'état sociale ne change point, la population n'augmente pas d'une manière indéfinie, mais *elle tend de plus en plus à devenir stationnaire**." P. F. Verhulst, a mathematical colleague of Quetelet's, was interested in the same things, and tried to give a mathematical shape to the same general conclusions; that is to say, he looked for a "*fonction retardatrice*" which should turn the Malthusian curve of geometrical progression into the S-shaped, or as he called it, the *logistic curve*, which should thus constitute the true "law of population," and thereby indicate (among other things) the limit above which the population was not likely to grow†.

Verhulst soon saw that he could only solve his problem in a preliminary and tentative way; "*la loi de la population nous est inconnue*, parce qu'on ignore la nature de la fonction qui sert de mesure aux obstacles qui s'opposent à la multiplication indéfinie de l'espèce humaine." The materials at hand were almost unbelievably scanty and poor. The French statistics were taken from documents "qui ont été reconnus entièrement fictifs"; in England the growth

* *Physique Sociale*, I, p. 27, 1835. But Quetelet's brief account is somewhat ambiguous, and he had in mind a body falling through a resistant medium—which suggests a limiting velocity, or limiting annual increment, rather than a *terminal value*. See Sir G. Udny Yule, The growth of population, *Journ. R. Statist. Soc.* LXXXVIII, p. 42, 1925.

† P. F. Verhulst, Notice sur la loi que la population suit dans son accroissement, *Correspondence math. etc.* publié par M. A. Quetelet, x, pp. 113–121, 1838; *Rech. math. sur la loi etc.*, *Nouv. Mém. de l'Acad. R. de Bruxelles*, XVIII, 38 pp., 1845; deuxième Mém., *ibid.* xx, 32 pp., 1847. The term *logistic curve* had already been used by Edward Wright; see *antea*, p. 135, *footnote*.

of the population was estimated by the number of births, and the births by the baptisms in the Church of England, “de manière que les enfants des dissidents ne sont point portés sur les registres officiels.” A law of population, or “*loi d’affaiblissement*” became a mere matter of conjecture, and the simplest hypothesis seemed to Verhulst to be, to regard “*cet affaiblissement comme proportionnel à l’accroissement de la population, depuis le moment où la difficulté de trouver de bonnes terres a commencé à se faire sentir**.”

Verhulst was making two assumptions. The first, which is beyond question, is that the rate of increase cannot be, and indeed is not, a constant; and the second is that the rate must somehow depend on (or be *some function* of) the population for the time being. A third assumption, again beyond question, is that the simplest possible function is a *linear function*. He suggested as the simplest possible case that, once the rate begins to fall (or once the struggle for existence sets in), it will fall the more as the population continues to grow; we shall have a *growth-factor* and a *retardation-factor* in *proportion to one another*. He was making early use of a simple differential equation such as Vito Volterra and others now employ freely in the general study of natural selection†.

The point where a struggle for existence first sets in, and where *ipso facto* the rate of increase begins to diminish, is called by Verhulst the *normal level* of the population; he chooses it for the origin of his curve, which is so defined as to be symmetrical on either side of this origin. Thus Verhulst’s law, and his logistic curve, owe their form and their precision and all their power to forecast the future to certain hypothetical assumptions; and the tentative solution arrived at is one “*sous le point de vue mathématique*‡.”

* *Op. cit.* p. 8.

† Besides many well-known papers by Volterra, see V. A. Kostitzin, *Biologie mathématique*, Paris, 1937. Cf. also, for the so-called “Malaria equations,” Ronald Ross, *Prevention of Malaria*, 2nd ed. 1911, p. 679; Martini, *Zur Epidemiologie d. Malaria*, Hamburg, 1921; W. R. Thompson, *C.R. CLXXIV*, p. 1443, 1922; C. N. Watson, *Nature*, cxi, p. 88, 1923.

‡ Verhulst goes on to say that “une longue série d’observations, non interrompues par de grandes catastrophes sociales ou des révolutions du globe, fera probablement découvrir la fonction retardatrice dont il vient d’être fait mention.” Verhulst simplified his problem to the utmost, but it is more complicated today than ever; he thought it impossible that a country should draw its bread and meat from overseas: “lors même qu’une partie considérable de la population pourrait être

The mathematics of the Verhulst-Pearl curve need hardly concern us; they are fully dealt with in Raymond Pearl's, Lotka's and other books. Verhulst starts, as Malthus does, with a population growing in geometrical progression, and so giving a logarithmic curve:

$$\frac{dp}{dt} = mp.$$

He then assumes, as his "loi d'affaiblissement," a coefficient of retardation (n) which increases as the population increases:

$$\frac{dp}{dt} = mp - np^2.$$

Integrating, $p = \frac{m}{n} \frac{1}{e^{-m(t+k)} + 1}.$

If the point of inflection be taken as the origin, $k = 0$; and again for $t = \infty$, $p = \frac{m}{n} = L$. We may write accordingly:

$$p = L \frac{1}{1 + e^{-mt}}.$$

Malthus had reckoned on a population doubling itself, if unchecked by want or "accident," every twenty-five years*; but fifty years after, Verhulst shewed that this "grande vitesse d'accroissement" was no longer to be found in France or Belgium or other of the older countries†, but was still being realised in the United States (Fig. 28). All over Europe, "le rapport de l'excès annuel des naissances sur les décès, à la population qui l'a fourni, va sans cesse en s'affaiblissant; de manière que l'accroissement annuel, dont la valeur absolue augmente continuellement lorsqu'il y a progression géométrique, paraît suivre une progression tout au plus arithmétique."

nourrie de blés étrangers, jamais un gouvernement sage ne consentira à faire dépendre l'existence de milliers de citoyens du bon vouloir des souverains étrangers." On this and other problems in the growth of a human population, see L. Hogben's *Genetic Problems*, etc., 1937, chap. vii. See also (*int. al.*) Warren S. Thompson and P. K. Whelpton, *Population Trends in the United States*, 1933; F. Lorimer and F. Osborn, *Dynamics of Population*, 1934, etc.

* An estimate based, like the rest of Malthus's arithmetic, on very slender evidence.

† In Quetelet's time the European countries, far from doubling in twenty-five years, were estimated to do so in from sixty years (Norway) to four hundred years (France); see M. Haushofer, *Lehrbuch der Statistik*, 1882.

The “celebrated aphorism” of Malthus was thus, and to this extent, confirmed*. In the United States, the Malthusian estimate of unrestricted increase continued to be realised for a hundred years after Malthus wrote; for the 3·93 millions of the U.S. census of 1790 were doubled three times over in the census of 1860, and four times over in that of 1890. A capital which doubles in twenty-five years has grown at 2·85 per cent. per annum, compound interest; the U.S. population did rather more, for it grew at fully 3 per cent. for fifty of those hundred years†.

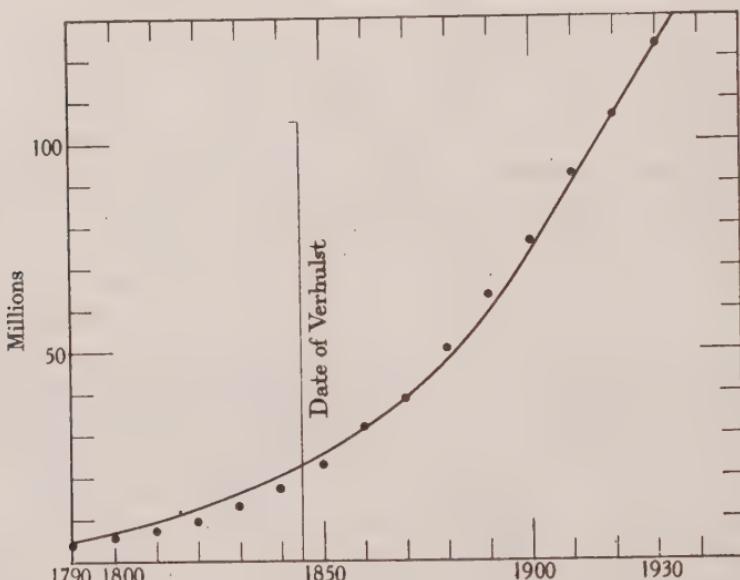


Fig. 28. Population of the United States, 1790–1930.

The population of the whole world and of every continent has increased during modern times, and the increase is large though the rate is low. The rate of increase has been put at about half-a-per-cent per annum for the last three hundred years—a shade more in Europe and a shade less in the rest of the world‡:

* *Op. cit.* 1845, p. 7.

† Verhulst foretold forty millions as the “extreme limit” of the population of France, and $6\frac{1}{2}$ millions as that of Belgium. The latter estimate he increased to 8 millions later on. The actual populations of France and Belgium at the present time are a little more than the ultimate limit which Verhulst foretold.

‡ From A. M. Carr-Saunders’ *World Population*, 1936, p. 30.

*An estimate of the population of the world
(After W. F. Willcox)*

	1650	1750	1800	1850	1900	Mean rate of increase
Europe	100	140	187	266	401	0.52% per annum
World total	545	728	906	1171	1608	0.49% „ „

Verhulst was before his time, and his work was neglected and presently forgotten. Only some twenty years ago, Raymond Pearl and L. J. Reed of Baltimore, studying the U.S. population as Verhulst had done, approached the subject in the same way, and came to an identical result; then, soon afterwards (about 1924), Raymond Pearl came across Verhulst's papers, and drew attention to what we now speak of as the Verhulst-Pearl law. Pearl and Reed saw, as Verhulst had done, that a "law of population" which should cover all the ups and downs of human affairs was not to be found; and yet the general form which such a law must take was plain to see. There must be a limit to the population of a region, great or small; and the curve of growth must sooner or later "turn over," approach the limit, and resolve itself into an S-shaped curve. The rate of growth (or annual increment) will depend (1) on the population at the time, and (2) on "the still unutilised reserves of population-support existing" in the available land. Here we have, to all intents and purposes, the growth-factor and retardation-factor of Verhulst, and they lead to the same formula, or the same differential equation, as his*.

A hundred years have passed since Verhulst dealt with the first U.S. census returns, and found them verifying the Malthusian expectation of a doubling every twenty-five years. That "grande vitesse d'accroissement" continued through five decennia; but it ceased some seventy years ago, and a retarding influence has been manifest through all these seventy years (Fig. 29). It is more recently, only after the census of 1910, that the curve seemed to be

* Raymond Pearl and L. J. Reed, on the Rate of growth of the population of the U.S. since 1790, and its mathematical representation, *Proc. Nat. Acad. Sci.* vi, pp. 275-288, 1920; *ibid.* viii, pp. 365-368, 1922; *Metron*, III, 1923. In the first edition of Pearl's *Medical Biometry and Statistics*, 1923 (2nd ed. 1930), Verhulst is not mentioned. See also his *Studies in Human Biology*, Baltimore, 1924, *Natural History of Population*, 1939, and other works.

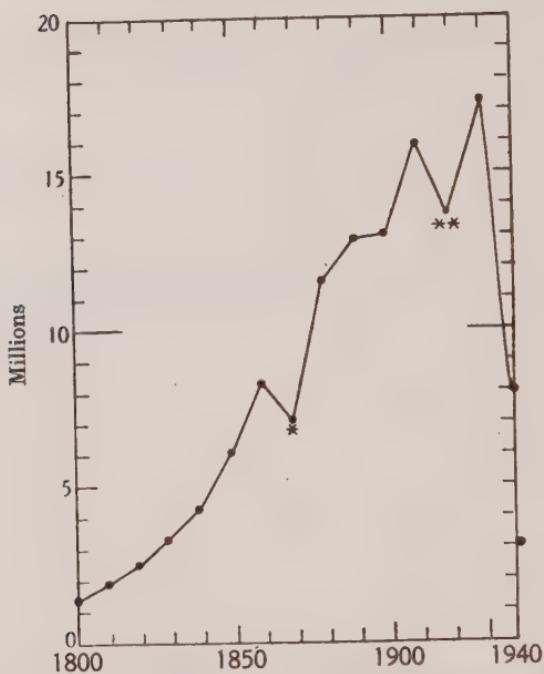


Fig. 29. Decennial increments of the population of the United States.
 * The Civil War. ** The "slump".

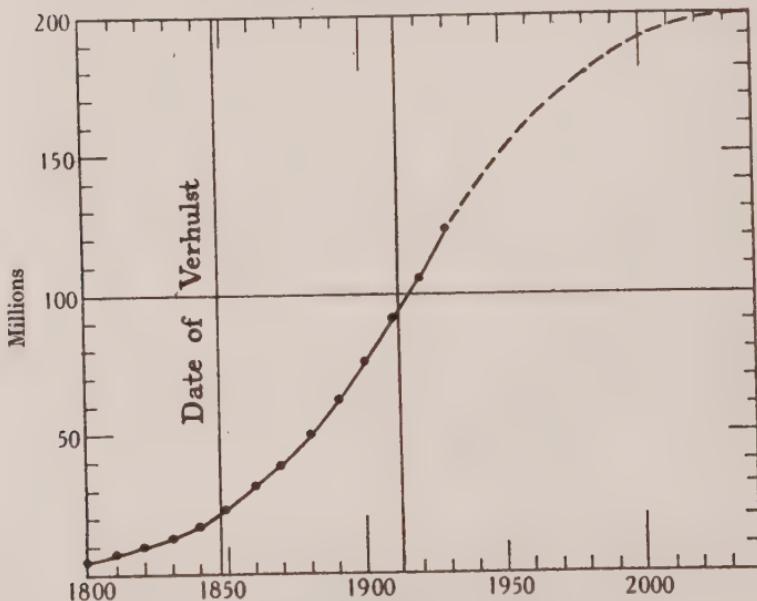


Fig. 30. Conjectural population of the United States,
 according to the Verhulst-Pearl Law.

finding its turning-point, or point of inflection; and only now, since 1940, can we say with full confidence that it has done so.

A hundred years ago the conditions were still relatively simple, but they are far from simple now. Immigration was only beginning to be an important factor; but immigrants made a quarter of the whole increase of the population of the United States during eighty of these hundred years*. Wars and financial crises have made their mark upon the curve; manners and customs, means and standards of living, have changed prodigiously. But the S-shaped curve makes its appearance through all of these, and the Verhulst-Pearl formula meets the case with surprising accuracy.

Population of the United States

Year	Population × 1000	Calculated by logistic curve (Udny Yule)	In ten years			Increase by multi- plication in 25 years
			No. of immigrants landed × 1000	Total increase of population × 1000	Percentage increase	
1790	3,929	3,929	—	—	—	—
1800	5,308	5,336	—	1,379	35·1	—
1810	7,240	7,223	—	1,932	36·4	—
1820	9,638	9,757	250	2,398	33·1	2·08
1830	12,866	13,109	228	3,228	33·5	2·05
1840	17,069	17,506	538	4,203	32·7	2·02
1850	23,192	23,192	1,427	6,123	35·9	2·06
1860	31,443	30,418	2,748	8,251	35·6	2·10
1870	38,558	39,372	2,123	7,115	32·6	1·91
1880	50,156	50,177	2,741	11,598	30·1	1·83
1890	62,948	62,769	5,249	12,792	25·5	1·80
1900	75,995	76,870	3,694	13,047	20·7	1·71
1910	91,972	91,972	8,201	15,977	21·0	1·63
1920	105,711	—	6,347	13,739	14·9	1·52
1930	122,975	—	—	17,264	16·1	1·46
1940	131,669	—	—	8,694	7·1	1·33

A colony of yeast or of bacteria is a population in its simplest terms, and Verhulst's law was rediscovered in the growth of a bacterial colony some years before Raymond Pearl found it in a population of men, by Colonel M'Kendrick and Dr Kesava Pai, who put their case very simply indeed†. The bacillus grows by geometrical

* Without counting the children born to those immigrants after landing, and before the next census return.

† A. G. M'Kendrick and M. K. Pai, The rate of multiplication of micro-organisms: a mathematical study, *Proc. R.S.E.* xxxi, pp. 649-655, 1911. (The period of generation in *B. coli*, answering to Malthus's twenty-five years for men, was found to be 22½ minutes.) (cf. also Myer Copans, *Journ. of Pathol. and Bacteriol.* xiv, p. 1, 1910 and H. G. Thornton, *Ann. of Applied Biology*, 1922, p. 265.)

progression so long as nutriment is enough and to spare; that is to say, the rate of growth is proportional to the number present:

$$\frac{dy}{dt} = by.$$

But in a test-tube colony the supply of nourishment is limited, and the rate of multiplication is bound to fall off. If a be the original concentration of food-stuff, it will have dwindled by time t to $(a - y)$. The rate of growth will now be

$$\frac{dy}{dt} = by(a - y),$$

which means that the rate of increase is proportional to the number of organisms present, and to the concentration of the food-supply. It is Verhulst's case in a nutshell; the differential equation so indicated leads to an S-shaped curve which further experiment confirms; and Sach's "grand period of growth" is seen to accomplish itself*.

The growth of yeast is studied in the everyday routine of a brewery. But the brewer is concerned only with the phase of unrestricted growth, and the rules of compound interest are all he needs, to find its rate or test its constancy. A population of 1360 yeast-cells grew to 3,550,000 in 35 hours: it had multiplied 2610 times. Accordingly,

$$\frac{\log 2610 = 3.417}{35} = 0.098 = \log 1.254.$$

That is to say, the population had increased at the rate of 25.4 per cent. *per hour*, during the 35 hours.

The time (t_2) required to *double* the population is easily found:

$$t_2 = \frac{\log 2}{\log 1.254} = \frac{0.301}{0.098} = 3.07 \text{ hours.}$$

* The sigmoid curve illustrates a theorem which, obvious as it may seem, is of no small philosophical importance, to wit, that a body starting from rest must, in order to attain a certain velocity, pass through all intermediate velocities on its way. Galileo discusses this theorem, and attributes it to Plato: "Platone avendo per avventura avuto concetto non potere alcun mobil passare dalla quiete ad alcun determinato grado di velocità... se non col passare per tutti gli altri gradi di velocità minori, etc."; *Discorsi e dimostrazioni*, ed. 1638, p. 254.

The duplication-period thus determined is known to brewers as the *generation-time*.

Much care is taken to ensure the maximal growth. If the yeast sink to the bottom of the vat only its upper layers enjoy unstinted nutriment; a potent retardation-factor sets in, and the exponential phase of the growth-curve degenerates into a premature horizontal asymptote. Moreover, both the yeast and the bacteria differ in this respect from the typical (or perhaps only simplified) case of man, that they not only begin to suffer want as soon as there comes to be a deficiency of any one essential constituent of their food*, but they also produce things which are injurious to their own growth and in time fatal to their existence. Growth stops long before the food-supply is exhausted; for it does so as soon as a certain balance is reached, depending on the kind or quality of the yeast, between the alcohol and the sugar in the cell†.

If we use the compound-interest law at all, we had better think of Nature's interest as being paid, not once a year nor once an hour as our elementary treatment of the yeast-population assumed, but continuously; and then we learn (in elementary algebra) that in time t , at rate r , a sum P increases to $Pert$, or $P_t = P_0e^{rt}$.

Applying this to the growth of our sample of 1360 yeast cells, we have

$$\log_e(P_t/P_0) = nr.$$

$P_t/P_0 = 2610$, $\log 2610 = 3.417$, which, multiplied by the modulus $2.303 = 7.868$. Dividing by $n = 35$, the number of hours,

$$7.868/35 = 0.225 = r.$$

The rate, that is to say, is 22.5 per cent. per hour, continuous compound interest. It becomes a well-defined physiological constant, and we may call it, with V. H. Blackman, an *index of efficiency*.

Our former result, for interest at hourly intervals, was 25.4 per

* According to Liebig's "law of the minimum."

† T. Carlson, Geschwindigkeit und Grösse der Hefevermehrung, *Biochem. Ztschr.* LVII, pp. 313-334, 1913; A. Slator, *Journ. Chem. Soc.* cxix, pp. 128-142, 1906; *Biochem. Journ.* vii, p. 198, 1913; O. W. Richards, *Ann. of Botany*, XLII, pp. 271-283, 1928; Alf Klem, *Hvalradets Skrifter*, nr. 7, pp. 55-91, Oslo, 1933; Per Ottestad, *ibid.* pp. 30-54. For optimum conditions of temperature, nutriment, pH, etc. see Oscar W. Richards, Analysis of growth as illustrated by yeast, *Cold Spring Harbour Symposia*, II, pp. 157-166, 1934.

cent.; there is no great difference between such short intervals and actual continuity, but there is a deal of difference between continuous payment and payment (say) once a year*. Certain sunflowers (*Helianthus*) were found to grow as follows, in thirty-seven days:

	Weight (gm.)		Compound interest rate (%)			
			Continuous		Discontinuous	
	Seedling	Plant	Per day	Per wk.	Per day	Per wk.
Giant sunflower	0.033	17.33	17.0	119	18.5	228 %
Dwarf sunflower	0.035	14.81	16.4	114	17.7	214 %

When the yeast population is allowed to run its course, it yields a simple S-shaped curve; and the curve of first differences derived

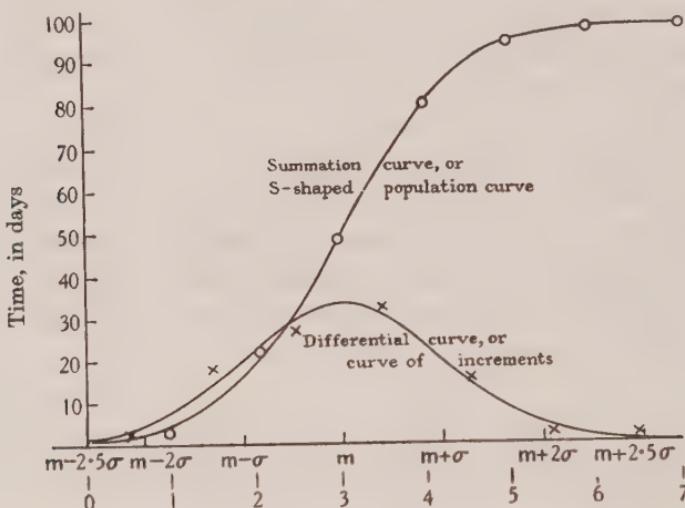


Fig. 31. The growth of a yeast-population. After Per Ottestad.

from this is, necessarily, a bell-shaped curve, so closely resembling the Gaussian curve that any difference between them becomes a delicate matter. Taking the numbers of the population at equal intervals of time from asymptotic start to asymptotic finish, we may treat this series of numbers like any other frequency distribution. Finding in the usual way the mode and standard deviation,

* Cf. V. H. Blackman, The compound interest law and plant growth, *Ann. of Botany*, xxxiii, pp. 353-360, 1919. The first papers on growth by compound interest in plants were by pupils of Noll in Bonn: e.g. von Kreusler, Wachstum der Maispflanze, *Landw. JB.* 1877-79; P. Gressler, *Substanz-quotienten von Helianthus*, Diss. Bonn, 1907 etc.

we draw the corresponding Gaussian curve; and the close "fit" between the observed population-curve and the calculated Gaussian curve is sufficiently shewn by Mr Per Ottestad's figure (Fig. 31). This is a very remarkable thing. We began to think of the curve of error as a function with which time had nothing to do, but here we have the same curve (or to all intents and purposes the same) with *time* for one of its coordinates. We might (I think) add one more to the names of the curve of error, and call it the curve of optimum; it represents on either hand the natural passage from best to worst, from likeliest to least likely.

A few flies (*Drosophila*) in a bottle illustrate the rise and fall of a population more complex than yeast, as Raymond Pearl has shewn*. The colony dwindles to extinction if food be withheld; if it be sufficient, the numbers rise in a smooth S-shaped curve; if it be plentiful and of the best, they end by fluctuating about an unstable maximum. "The population waves up and down about an average size," as Raymond Pearl says, as Herbert Spencer had foreseen†, and as Vito Volterra's differential equations explain. The growth-rate slackens long before the hunger line is reached; crowding affects the birth-rate as well as the death-rate, and a bottleful of flies produces fewer and fewer offspring *per pair* the more flies we put into the bottle‡. It is true also of mankind, as Dr William Farr was the first to shew, that overcrowding diminishes the birth-rate and shortens the "expectation of life§." It happened so in the United States, *pari passu* with the growth of immigration, incipient congestion acting (or so it seemed) as an obstacle, or a deterrent, to the large families of former days. Nevertheless, children still pullulate in the slums. The struggle for existence is no simple affair, and things happen which no mathematics can foretell.

* Raymond Pearl and S. L. Parker, in *Proc. Nat. Acad. Sci.* viii, pp. 212-219, 1922; Pearl, *Journ. Exper. Zool.* lxiii, pp. 57-84, 1932.

† "Wherever antagonistic forces are in action, there tends to be alternate predominance."

‡ In certain insects an optimum density has been observed; a certain amount of crowding accelerates, and a greater amount retards, the rate of reproduction. Cf. D. Stewart MacLagan, Effect of population-density on rate of reproduction, *Proc. R. S. (B)*, cxi, p. 437, 1932; W. Goetsch, Ueber wachstumhemmende Factoren, *Zool. Jahrb. (Allg. Zool.)*, xlvi, pp. 799-840, 1928.

§ Dr W. Farr, *Fifth Report of the Registrar-General*, 1843, p. 406 (2nd ed.).

An analogous S-shaped curve, given by the formula $L_x = kf^x$, was introduced by Benjamin Gompertz in 1825*; it is well known to actuaries, and has been used as a curve of growth by several writers in preference to the logistic curve. It was devised, and well devised, to express a "law of human mortality", and to signify the number surviving at any given age (x), "if the average exhaustions of a man's power to avoid death were such that at the end of infinitely small intervals of time he lost equal portions (i.e. *equal proportions*) of his remaining power to oppose destruction." The principle involved is very important. Death comes by two roads. One is by chance or accident, the other by a steady deterioration, or exhaustion, or growing inability to withstand destruction; and exhaustion comes (roughly speaking) as by the repeated strokes of an air-pump, for the life-tables shew mortality increasing in geometrical progression, at least to a first approximation and over considerable periods of years. Gompertz relied wholly on the experience of "life-contingencies," but the same deterioration of bodily energies is plainly visible as growth itself slows down; for we have seen how growth-rate in infancy is such as is never afterwards attained, and we may speak of growth-energy and its gradual loss or decrement, by an easy but significant alteration of phrase. To deal with the declining growth-rate, as Gompertz did with the falling expectation of life, and so to measure the remaining energy available from time to time, would be a greater thing than to record mere weights and sizes; it raises the problem from mere change of physical magnitudes to an estimation of the falling or fluctuating physiological energies of the body†. We have seen how in only

* Benjamin Gompertz, On the nature of the function expressive of the law of human mortality, *Phil. Trans.* xxxvi, pp. 513–585, 1825. First suggested for use in growth-problems by Sewall Wright, *Journ. Amer. Statist. Soc.* xxii, p. 493, 1926. See also C. P. Winsor, The Gompertz curve as a growth curve, *Proc. Nat. Acad. Sci.* xvii, pp. 1–8, 1932; cf. (*int. al.*) G. R. Davies, The growth curve, *Journ. Amer. Statist. Soc.* xxii, pp. 370–374, 1927; F. W. Weymouth and S. H. Thompson, Age and growth of the Pacific cockle, *Bull. Bureau Fisheries*, xlvi, pp. 633–641, 1930–31; also Weymouth, McMillen and Rich, in *Journ. Exp. Biol.* viii, p. 228, 1931.

† A bold attempt to treat the question from the physiological side, and on Gompertz's lines, was made only the other day by P. B. Medawar, The growth, growth-energy and ageing of the chicken's heart, *Proc. R.S. (B)*, cxxix, pp. 332–355, 1940. Cf. James Gray, The kinetics of growth, *Journ. Exp. Biol.* vi, pp. 248–274, 1929.

few and simple cases can a simple curve or single formula be found to represent the growth-rate of an organism; and how our curves mostly suggest cycles of growth, each spurt or cycle enduring for a time, and one following another. Nothing can be more natural from the physiological point of view than that energy should be now added and now withheld, whether with the return of the seasons or at other stages on the eventful journey from childhood to manhood and old age.

The symmetry, or lack of skewness, in the Verhulst-Pearl logistic curve is a weak point rather than a strong; the Gompertz curve is a skew curve, with its point of inflexion not half-way, but about one-third of the way between the asymptotes. But whether in this or in the logistic or any other equation of growth, the precise point of inflexion has no biological significance whatsoever. What we want, in the first instance, is an **S**-shaped curve with a variable, or modifiable, degree of skewness. After all, the same difficulty arises in all the use we make of the Gaussian curve: which has to be eked out by a whole family of skew curves, more or less easily derived from it. We are far from being confined to the Gaussian curve (*sensu stricto*) in our studies of biological probability, or to the logistic curve in the study of population.

Yet another equation has been proposed to the **S**-shaped curve of growth, by Gaston Backman, a very diligent student of the whole subject. The rate of growth is made up, he says, of three components: a constant velocity, an acceleration varying with the time, and a retardation which we may suppose to vary with the square of the time. Acceleration would then tend to prevail in the earlier part of the curve, and retardation in the latter, as in fact they do; and the equation to the curve might be written:

$$\log H = k_0 + k_1 \log T - k_2 \log^2 T.$$

The formula is an elastic one, and can be made to fit many an **S**-shaped curve; but again it is empirical.

The logistic curve, as defined by Verhulst and by Pearl, has doubtless an interest of its own for the mathematician, the statistician and the actuary. But putting aside all its mathematical details and all arbitrary assumptions, the generalised **S**-shaped curve is a very symbol of childhood, maturity and age, of activity which rises to

fall again, of growth which has its sequel in decay. The growth of a child or of a nation; the history of a railway*, or the speed between stations of a train; the spread of an epidemic†, or the evolutionary survival of a favoured type‡—all these things run their course, in its beginning, its middle and its end, after the fashion of the S-shaped curve. That curve represents a certain common pattern among Nature's "mechanisms," and is (as we have said before), a "mécanisme commun aux phénomènes disparates§."

At the same time—and this is a very interesting part of the story—the S-shaped curve is no other than what Galton called a *curve of distribution*, that is to say a curve of integration or summation-curve, whose differential is closely akin to the Gaussian curve of error.

Such, to a first approximation, is our S-shaped population-curve, and such are the many phenomena which, to a first approximation, it helps us to compare. But it is *only* to a first approximation that we compare the growth of a population with that of an organism, or for that matter of one organism or one population with another. There are immense differences between a simple and a complex organism, between a primitive and a civilised population. The yeast-plant gives a growth-curve which we can analyse; but we must fain be content with a qualitative description of the growth of a complex organism in its complex world||.

There is a simplicity in a colony of protozoa and a complexity in a warm-blooded animal, a uniformity in a primitive tribe and a heterogeneity in a modern state or town, which affect all their economies and interchanges, all the relations between *milieu interne* and *externe*, and all the coefficients in any but the simplest equations of growth which we can ever attempt to frame. Every growth-problem becomes at last a specific one, running its own course for its own reasons. Our curves of growth are all alike—but no two are ever

* Raymond Pearl, *Amer. Nat.* LXI, pp. 289–318, 1927.

† Ronald Ross, *Prevention of Malaria* (2nd ed.), 1911, p. 679.

‡ J. B. S. Haldane, *Trans. Camb. Phil. Soc.* XXIII, pp. 19–41, 1924.

§ Cf. (*int. al.*) J. R. Miner's Note on birth-rate and density in a logistic population, *Human Biology*, IV, p. 119, 1932; and cf. Lotka, *ibid.* III, p. 458, 1931.

|| Cf. (*int. al.*) C. E. Briggs, Attempts to analyse growth-curves, *Proc. R.S. (B)*, cxii, pp. 280–285, 1928.

the same. Growth keeps calling our attention to its own complexity. We see it in the rates of growth which change with age or season, which vary from one limb to another; in the influence of peace and plenty, of war and famine; not least in those composite populations whose own parts aid or hamper one another, in any form or aspect of the struggle for existence. So we come to the differential equations, easy to frame, more difficult to solve, easy in their first steps, hard and very powerful later on, by which Lotka and Volterra have shewn how to apply mathematics to evolutionary biology, but which lie just outside the scope of this book*.

An important element in a population, and one seldom easy to define, is its *age-composition*. It may vary one way or the other; for the diminution of a population may be due to a decrease in the birth-rate, or to an increasing mortality among the old. A remarkable instance is that of the food-fishes of the North Sea. Their birth-rate is so high that the very young fishes remain, to all appearance, as numerous as ever; those somewhat older are fewer than before, and the old dwindle to a fraction of what they were wont to be.

The rate of growth in other organisms

The rise and fall of growth-rate, the acceleration followed by retardation which finds expression in the S-shaped curve, are seen alike in the growth of a population and of an individual, and in most things which have a beginning and an end. But the law of large numbers smooths the population-curve; the individual life draws attention to its own ups and downs; and the characteristic sigmoid curve is only seen in the simpler organisms, or in parts or "phases" of the more complex lives. We see it at its simplest in the simple growth-cycle, or single season, of an annual plant, which cycle draws to its end at flowering; and here not only is the curve simple, but its amplitude may sometimes be very large. The giant *Heracleum* and certain tall varieties of Indian corn grow to twelve feet

* See (*int. al.*) A. J. Lotka, *Elements of Physical Biology*, Baltimore, 1925; *Théorie analytique des associations biologiques*, Paris, 1934; Vito Volterra, *Leçons sur la théorie mathématique de la lutte pour la vie*, 1931; Volterra et U. d'Ancona, *Les associations biologiques au point de vue mathématique*, 1935; V. A. Kostitzin, *op. cit.*; etc.

high in a summer; the kudzu vine (*Pueraria*) may grow twelve inches in twenty-four hours, and some bamboos are said to have grown twenty feet in three days (Figs. 32, 33).

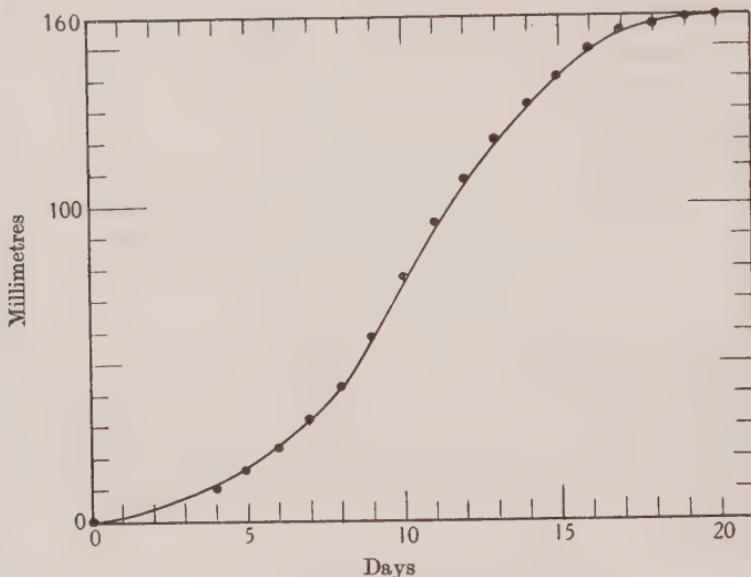


Fig. 32. Growth of Lupine. After Pfeffer.

Growth of Lupinus albus. (From G. Backman, after Pfeffer)

Day	Length (mm.)	Difference	Day	Length (mm.)	Difference
4	10.5	—	14	132.3	12.2
5	16.3	5.8	15	140.6	8.3
6	23.3	7.0	16	149.7	9.1
7	32.5	9.2	17	155.6	5.9
8	42.2	9.7	18	158.1	2.5
9	58.7	14.5	19	160.6	2.5
10	77.9	19.2	20	161.4	0.8
11	93.7	15.8	21	161.6	0.2
12	107.4	13.7			
13	120.1	12.7			

In the pre-natal growth of an infant the S-shaped curve is clearly seen (Fig. 18); but immediately after birth another phase begins, and a third is implicit in the spurt of growth which precedes puberty. In short, it is a common thing for one wave of growth (or *cycle*, as

some call it) to succeed another, whether at special epochs in a lifetime, or as often as winter gives place to spring*.

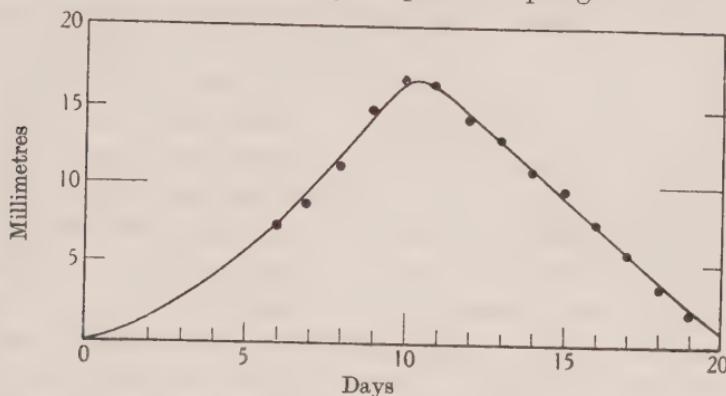


Fig. 33. Growth of Lupine: daily increments.

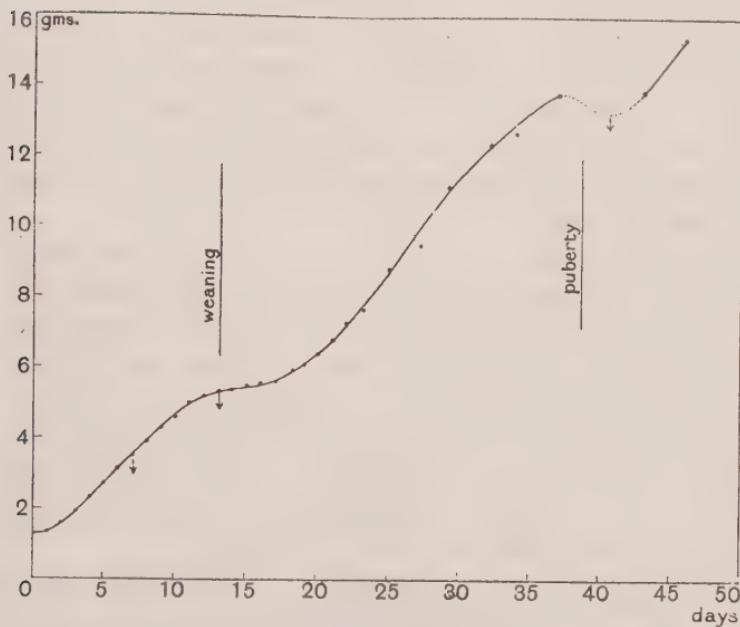


Fig. 34. Growth in weight of a mouse. After W. Ostwald.

In the accompanying curve of weight of the mouse (Fig. 34) we see a slackening of the rate of growth when the mouse is about a fortnight old, at which epoch it opens its eyes, and is weaned soon

* W. Pfeffer, *Pflanzenphysiologie*, 1881, Bd. II, p. 78; A. Bennett, On the rate of growth of the flower-stalk of *Vallisneria spiralis* and of *Hyacinthus*, *Trans. Linn. Soc.* (2), I, Botany, pp. 133, 139, 1880; cited by G. Backman, *Das Wachstums-*

after. At six weeks old there is another well-marked retardation; it follows on a rapid spurt, and coincides with the epoch of puberty*.

In arthropod animals growth is apt to be especially discontinuous, for their bodies are more or less closely confined until released by the casting of the skin. The blowfly has its striking metamorphoses, yet its growth is wellnigh continuous; for its larval skin is too thin and delicate to impede growth in the usual arthropod way. But in a thick-skinned grasshopper or hard-shelled crab growth goes by fits and starts, by steps and stairs, as Réaumur was the first to shew; for, speaking of insects†, he says: "Peut-être est-il vrai généralement que leur accroissement, ou au moins leur plus considérable accroissement, ne se fait que dans le temps qu'ils muent, ou pendant un temps assez court après la mue. Ils ne sont obligés de quitter leur enveloppe que parce qu'elle ne prend pas un accroissement proportionné à celui que prennent les parties qu'elle couvre." All the visible growth of the lobster takes place once a year at moulting-time, but he is growing in weight, more or less, all along. He stores up material for months together; then comes a sudden rush of water to the tissues, the carapace splits asunder, the lobster issues forth, devours his own exuviae, and lies low for a month while his new shell hardens.

The silkworm moults four times, about once a week, beginning on the sixth or seventh day after hatching. There is an arrest or retardation of growth before each moult, but our diagram (Fig. 35) is too small to shew the slight ones which precede the first and

problem, in *Ergebnisse d. Physiologie*, xxxiii, pp. 883–973, 1931. These two cases of *Lupinus* and *Vallisneria*, are among the many which lend themselves easily to Backman's growth-formula, viz. *Lupinus*, $\log p = -2.40 + 1.48 \log T - 6.61 \log^2 T$ and *Vallisneria*, $\log p = +1.28 + 4.51 \log T - 2.62 \log^2 T$. See for an admirable résumé of facts, Wolfgang Ostwald, *Ueber die zeitliche Eigenschaften der Entwicklungsvorgänge* (71 pp.), 1908 (in Roux's *Vorträge*, Heft v); and many later works.

* Cf. R. Robertson, Analysis of the growth of the white mouse into its constituent processes, *Journ. Gen. Physiology*, viii, p. 463, 1926. Also Gustav Backman, Wachstum d. w. Maus, *Lunds Univ. Arsskrift*, xxxv, Nr. 12, 1939, with copious bibliography. Backman analyses the complicated growth-curve of the mouse into one main and three subordinate cycles, two of which are embryonic. Cf. St Loup, Vitesse de croissance chez les souris, *Bull. Soc. Zool. Fr.* xviii, p. 242, 1893; E. Le Breton and G. Schäfer, *Trav. Inst. Physiol. Strasburg*, 1923; E. C. MacDowell, Growth-curve of the suckling mouse, *Science*, lxviii, p. 650, 1928; cf. *Journ. Gen. Physiol.* xi, p. 57, 1927; Ph. l'Héritier, Croissance... dans les souris, *Ann. Physiol. et Phys. Chemie*, v, p. i, 1929.

† *Mémoires*, iv, p. 191.

second. Before entering on the pupal or chrysalis stage, when the worm is about seven weeks old, a remarkable process of purgation

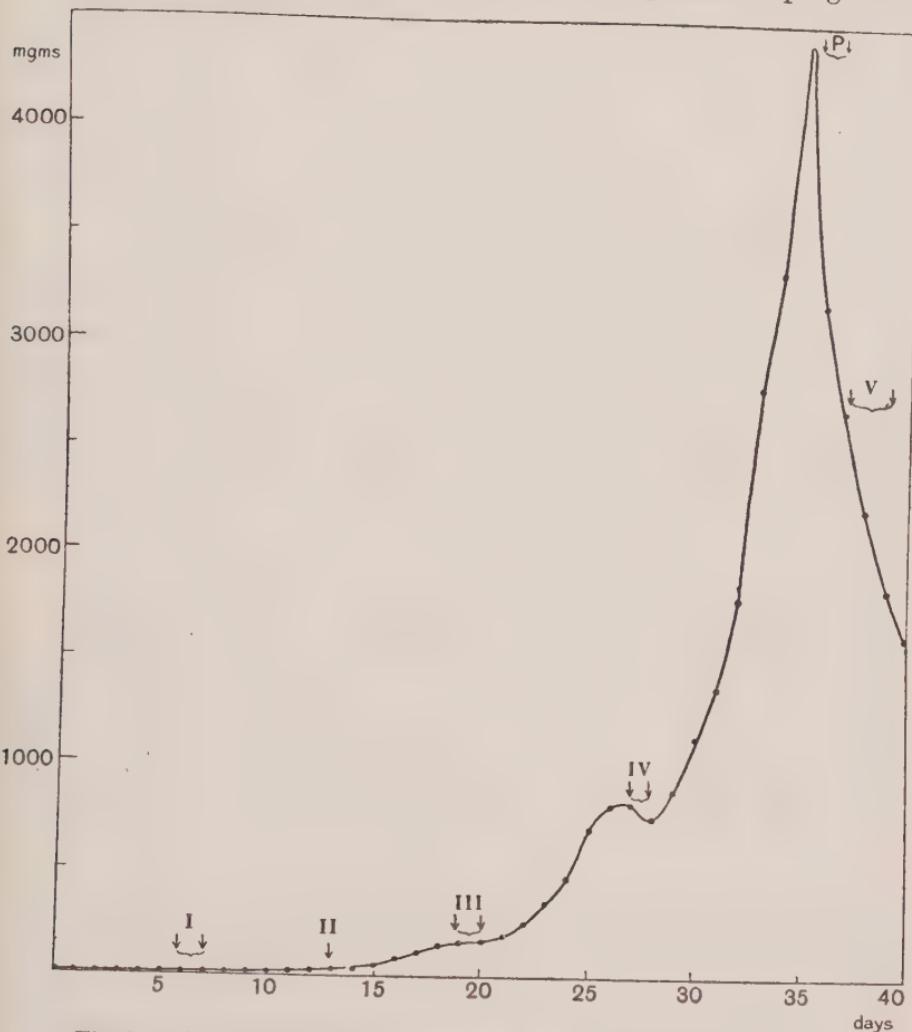


Fig. 35. Growth in weight of silkworm. From Ostwald, after Luciani and Lo Monaco.

takes place, with a sudden loss of water, and of weight, which becomes the most marked feature of the curve*. That the meta-

* Luciani e Lo Monaco, *Arch. Ital. de Biologie*, xxvii, p. 340, 1897; see also Z. Kuwana, Statistics of the body-weight of the silkworm, *Japan. Journ. Zool.* vii, pp. 311-346, 1937. Westwood, in 1838, quoted similar data from Count Dandolo: according to whom 100 silkworms weigh on hatching 1 grain; after the first four moults, 15, 94, 270 and 1085 grains; and 9500 grains when full-grown.

morphoses of an insect are but phases in a process of growth was clearly recognised by Swammerdam, in the *Biblia Naturae**.

A stick-insect (*Dexippus*) moults six or seven times in as many months; it lengthens at every moult, and keeps of the same length until the next. Weight is gained more evenly; but, before each moult the creature stops feeding for a day or two, and a little weight is lost in the casting of the skin. After its last moult the stick-insect puts on more weight for a while; but growth soon draws to an end, and the bodily energies turn towards reproduction.

We have careful measurements of the locust from moult to moult, and know from these the *relative* growth-rates of its parts, though we cannot plot these dimensions against *time*. Unlike the metamorphosis of the silkworm, the locust passes through five larval stages (or "instars") all much alike, until in a final moult the "hoppers" become winged. Here are three sets of measurements, of limbs and head, from stage to stage†.

Growth of locust, from one moult to another

Stage	Length (mm.)			Percentage-growth			Ratios		
	Anterior femur	Median femur	Head	Anterior femur	Median femur	Head	Anterior femur	Median femur	Head
I	1.44	3.98	1.44	—	—	—	1	2.76	1.00
II	2.06	5.69	1.94	1.44	1.43	1.35	1	2.76	0.94
III	3.08	8.22	2.70	1.40	1.44	1.39	1	2.67	0.88
IV	4.53	11.94	3.71	1.47	1.45	1.37	1	2.76	0.82
V	6.40	17.22	4.89	1.41	1.44	1.32	1	2.69	0.76
Adult	8.03	22.85	5.59	1.25	1.33	1.14	1	2.84	0.70

As a matter of fact the several parts tend to grow, *for a time*, at a steady rate of compound interest, which rate is not identical for head and limbs, and tends in each case to fall off in the final moult, when material has to be found for the wings. Some fifty years ago, W. K. Brooks found the larva of a certain crab (*Squilla*) increasing at each moult by a quarter of its own length; and soon after H. G. Dyar declared that caterpillars grow likewise, from moult to moult, by geometrical progression‡. This tendency to a compound-

* 1737, pp. 6, 579, etc.

† A. J. Duarte, Growth of the migratory locust, *Bull. Ent. Res.* xxix, pp. 425–456, 1938.

‡ W. K. Brooks, *Challenger Report on the Stomatopoda*, 1886; H. G. Dyar, Number of moults in lepidopterous larvae, *Psyche*, v, p. 424, 1896.

interest rate in the growth and metamorphosis of insects is known as Dyar's, sometimes as Brooks's, law. According to Przibram, an insect moults as soon (roughly speaking) as cell-division has doubled the number of cells throughout the larval body. That being so, each stage or instar should weigh twice as much as the one before, and each linear dimension should increase by $\sqrt[3]{2}$, or 1.26 times—a measure identical, to all intents and purposes, with Brooks's first estimate. As a *first rough approximation* the rule has a certain value. According to Duarte's measurements the locust's total weight increases from moult to moult by 2.31, 2.16, 2.42, 2.35, 2.21, or a mean increase of 2.29, the cube-root of which is 1.32. Each phase is doubled and more than doubled, in passing to the next*, but Przibram's estimate is not far departed from.

Whatever truth Przibram's law may have in insects, or (as Fowler asserted) in the Ostracods, it would seem to have none in the Cladocera and this for the sufficient reason that the shell (on which the form of the creature depends) goes on growing all through post-embryonic life without further division or multiplication of its cells, but only by their individual, and therefore collective, enlargement†.

Shells are easily weighed and measured and their various dimensions have been often studied: only in oysters, pearl-oysters and the like, have they been so kept under observation that their actual age is known. The oyster-shell grows for a few weeks in spring just before spawning time, and again in autumn when spawning is over; its growth is imperceptible at other times‡.

* Cf. H. Przibram and F. Megusar, Wachstumsmessungen an *Sphodromantis*, *Arch. f. Entw. Mech.* xxxiv, pp. 680–741, 1912; etc. How the discrepancy is accounted for, by Bodenheimer and others, need not concern us here. But cf. P. P. Calvert, On rates of growth among...the Odonata, *Proc. Amer. Phil. Soc.* lxviii, pp. 227–274, 1929, who finds growth faster in nine cases out of ten than Przibram's rule lays down.

Millet asserts, in support of Przibram's law, that in spiders mitotic cell-division is confined to the epoch of the moult, and is then manifested throughout most of the tissues (*Bull. de Biologie (Suppl.)*, viii, p. 1, 1926). On the other hand, the rule is rejected by R. Gurney, Rate of growth in Copepoda, *Int. Rev. Hydrobiol.* xxii, pp. 189–27, 1929; Nobumasa Kagi, Growth-curves of insect-larvae, *Mem. Coll. Agric. Kyoto*, No. 1, 1926; and others.

† Cf. W. Rammer, Ueber die Gültigkeit des Brooksschen Wachstumsgesetzes bei den Cladoceren, *Arch. f. Entw. Mech.* cxxi, pp. 111–127, 1930.

‡ Cf. J. H. Orton, Rhythmic periods...in Ostrea, *Journ. Mar. Biol. Assoc.* xv, pp. 365–427, 1928; *Nature*, March 2, 1935, p. 340.

The window-pane oyster in Ceylon (*Placuna placenta*) has been kept under observation for eight years, during which it grows from two inches long to six (Fig. 36). The young grow quickly, and slow down asymptotically towards the end; an S-shaped beginning to the growth-curve has not been seen, but would probably be found in the growth of the first year. Changes of shape as growth goes on are hard to see in this and other shells; rather is it characteristic of

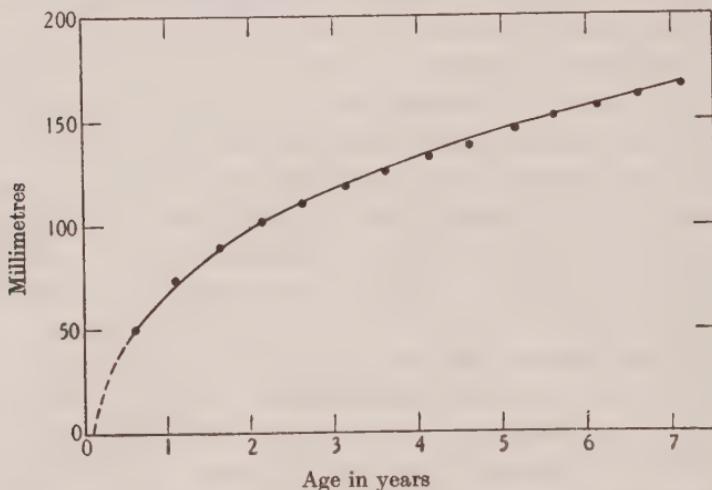


Fig. 36. Growth of the window-pane oyster; short diameter of the shell.
From Pearson's data.

them to keep their shape from first to last unchanged. Nevertheless, slight changes are there; in the window-pane oyster the shell grows somewhat rounder; in seven or eight years the one diameter multiplies (roughly speaking) by eleven, and the other by ten*.

Window-pane oysters (*Placuna*)

Short diameter (mm.)	Long diameter (mm.)	Ratio
15·0	17·6	1·17
65·0	70·5	1·09
102·5	109·7	1·07
132·5	139·9	1·06
167·5	175·2	1·05

The American slipper-limpet has lately and quickly become a pest on English oyster-beds. Its mode of growth is interesting, though

* Joseph Pearson, The growth-rate... of *Placuna placenta*, *Ceylon Bulletin*, 1928.

the actual rate remains unknown. It grows a little longer and narrower with age. Its weight-length coefficient (of which we shall have more to say presently) increases as time goes on, and appears to follow a wavy course which might be accounted for if the shell grew thinner and then thicker again, as if ever so little more lime were secreted at one season than another. The growth of a shell, or the deposition of its calcium carbonate, is much influenced by temperature; clams and oysters enlarge their shells only so long as the temperature stands above a certain specific minimum, and the mean size of the same limpet is very different in Essex and in the United States*. Curious peculiarities of growth have been discovered in slipper-limpets. Young limpets clustered round an old female grow slower than others which live solitary and apart. The solitary forms become in turn male, hermaphrodite and at last female, but the gregarious or clustered forms develop into males, and so remain; development of male characters and duration of the male phase depend on the presence or absence of a female in the near neighbourhood.

*Measurements of slipper-limpets
(From J. H. Fraser's data, epitomised)*

No. measured	Mean length (mm.)	Breadth (mm.)	Ratio L/B	Weight (gm.)	W/L^3
3	15.3	8.8	1.74	0.33	92
8	17.6	9.8	1.80	0.46	84
9	19.4	10.5	1.85	0.63	88
16	21.5	11.5	1.87	0.77	77
18	23.5	12.5	1.88	1.04	80
41	25.5	13.7	1.86	1.37	85
91	27.4	14.5	1.89	1.81	88
125	39.4	15.4	1.91	2.33	92
98	31.4	16.5	1.90	3.22	104
70	33.6	17.8	1.89	3.61	95
38	35.5	18.6	1.90	4.28	95
10	37.3	19.5	1.91	4.95	95
1	32.1	19.4	2.01	5.35	90
		Mean	1.87		89.3

* Cf. J. H. Fraser, On the size of *Urosalpinx* etc., *Proc. Malacol. Soc.* xix, pp. 243-254, 1931. Much else is known about the growth of various limpets, their seasonal periodicities, the change of shape in certain species, and other matters; cf. E. S. Russell, Growth of *Patella*, *P.Z.S.* cxcix, pp. 235-253; J. H. Orton, *Journ. Mar. Biol. Assoc.* xv, pp. 277-288, 1929; Noboru Abe, *Sci. Rep. Tohoku Imp. Univ. Biol.* vi, pp. 347-363, 1932, and Okuso Hamai, *ibid.* xii, pp. 71-95, 1937.

The growth of the tadpole* is likewise marked by epochs of retardation, and finally by a sudden and drastic change (Fig. 37). There is a slight diminution in weight immediately after the little larva frees itself from what remains of the egg; there is a retardation

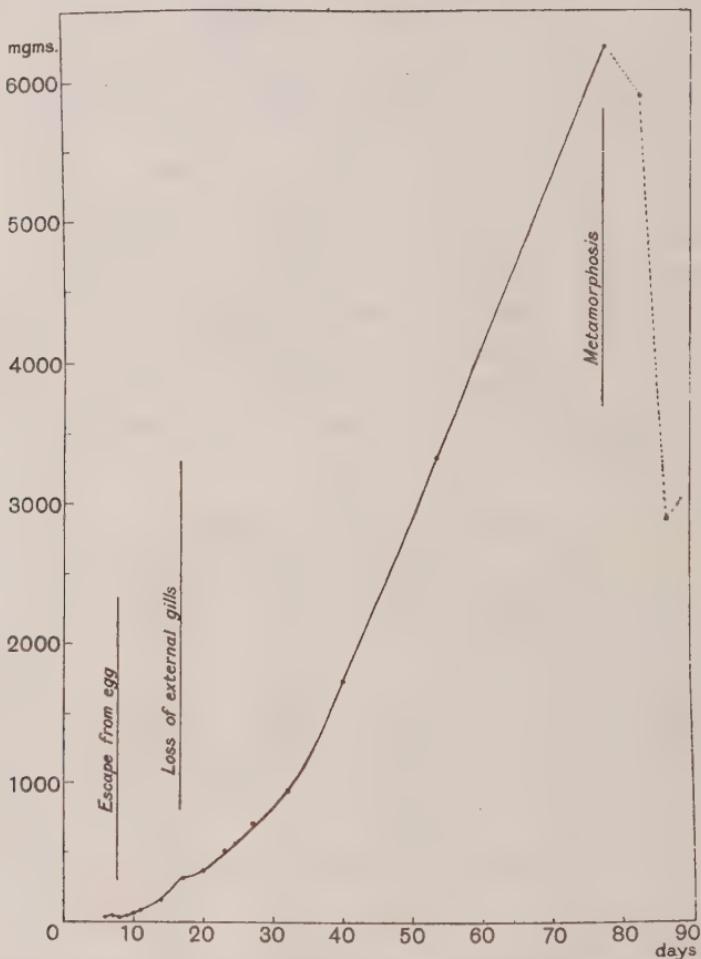


Fig. 37. Growth in weight of tadpole. From Ostwald, after Schaper.

of growth about ten days later, when the external gills disappear; and finally the complete metamorphosis, with the loss of the tail, the growth of the legs and the end of branchial respiration, brings about a loss of weight amounting to wellnigh half the weight of the full-grown

* Cf. (*int. al.*) Barfurth, Versüche über die Verwandlung der Froschlarven, *Arch. f. mikrosk. Anat.* XXIX, 1887.

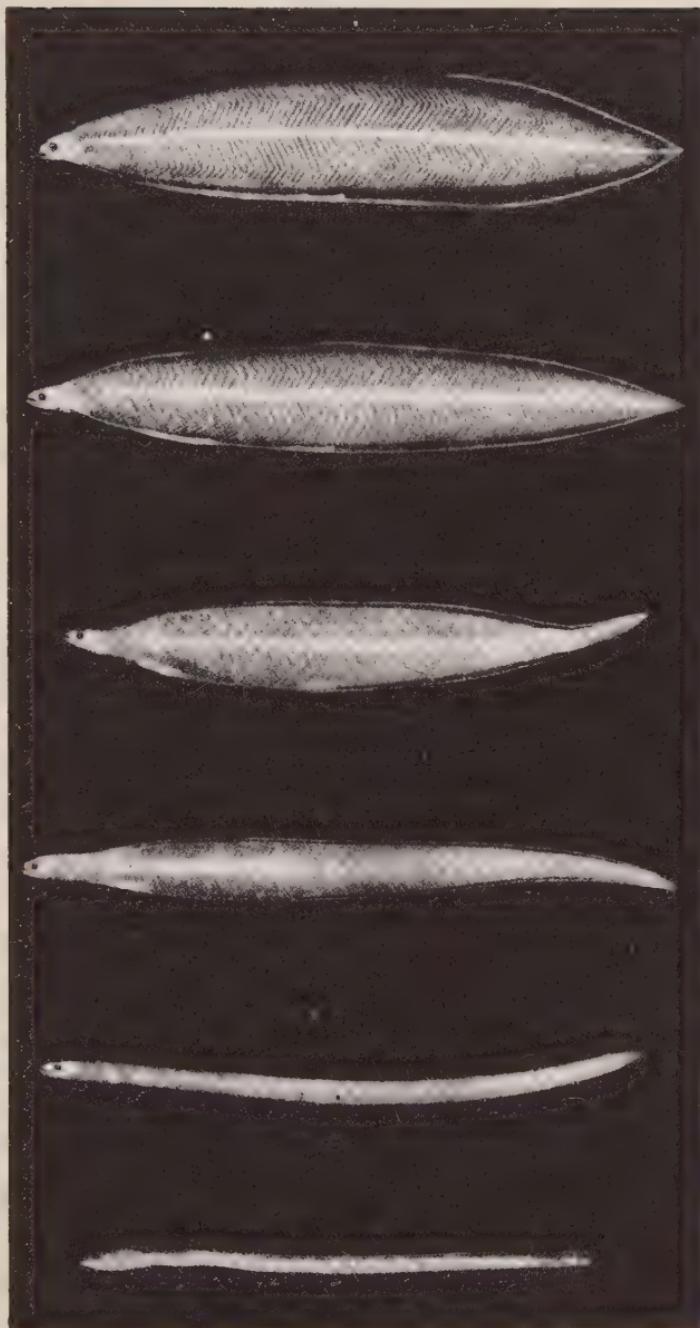


Fig. 38. Development of eel: from *Leptocephalus* larvae to young elver.
After Johannes Schmidt.

larva. At the root of the matter lies the simple fact that metamorphosis involves wastage of tissue, increase of oxidation, expenditure of energy and the *doing of work*. While as a general rule the better the animals be fed the quicker they grow and the sooner they metamorphose, Barfurth has pointed out the curious fact that a short spell of starvation, just before metamorphosis is due, appears to hasten the change.

The negative growth; or actual loss of bulk and weight which often, and perhaps always, accompanies metamorphosis, is well shewn in the case of the eel*. The contrast of size is great between the flattened, lancet-shaped *Leptocephalus* larva and the little black, cylindrical, almost thread-like elver, whose magnitude is less than that of the *Leptocephalus* in every dimension, even at first in length (Fig. 38), as Grassi was the first to shew.

The lamprey's case is hardly less remarkable. The larval or Ammocoete stage lasts for three years or more, and metamorphosis, though preceded by a spurt of growth, is followed by an actual decrease in size. The little brook lamprey neither feeds nor grows after metamorphosis, but spawns a few months later and then dies; but the big sea-lampreys become semi-parasitic on other fishes, and live and grow to an unknown age†.

Such fluctuations as these are part and parcel of the general flux of physiological activity, and suggest a finite stock of energy to be spent, now more now less, on growth and other modes of expenditure. The larger fluctuations are special interruptions in a process which is never continuous, but is perpetually varied by rhythms of various kinds and orders. Hofmeister shewed long ago, for instance, that *Spirogyra* grows by fits and starts, in periods of activity and rest alternating with one another at intervals of so many minutes‡ (Fig. 39). And Bose tells us that plant-growth proceeds by tiny and perfectly rhythmical pulsations, at intervals of a few seconds of time.

* Johannes Schmidt, Contributions to the life-history of the eel, *Rapports du Conseil Intern. pour l'exploration de la mer*, v, pp. 137–274, Copenhagen, 1906; and other papers.

† Cf. (*int. al.*) A. Meek, The lampreys of the Tyne, *Rep. Dove Marine Laboratory* (N.S.), vi, p. 49, 1917; cf. L. Hubbs, in *Papers of the Michigan Academy*, iv, p. 587, 1924.

‡ *Die Lehre der Pflanzenzelle*, 1867. Cf. W. J. Koningsberger, *Tropismus und Wachstum* (Thesis), Utrecht, 1922.

A crocus grows, he says, by little jerks, each with an amplitude of about 0.002 mm., every twenty seconds or so, each increment being followed by a partial recoil* (Fig. 40). If this be so we have come

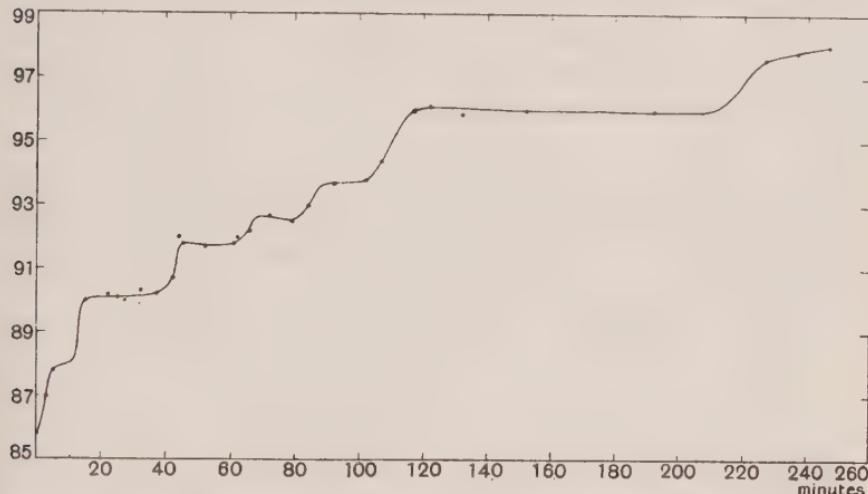


Fig. 39. Growth in length (mm.) of Spirogyra. From Ostwald, after Hofmeister.

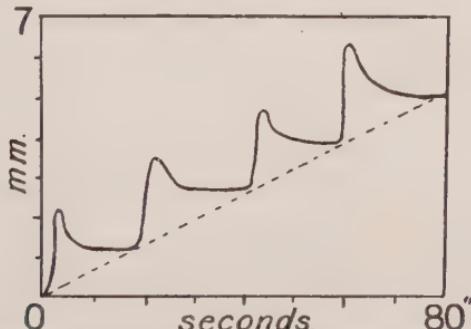


Fig. 40. Pulsations of growth in Crocus, in micro-millimeters.
After Bose.

down, so to speak, from a principle of continuity to a principle of discontinuity, and are face to face with what we might call, by rough analogy, "quanta of growth." We seem to be in touch with things of another order than the subject of this book†.

* J. C. Bose, *Plant Response*, 1906, p. 417; *Growth and Tropic Movements of Plants*, 1929.

† There is an apparent and perhaps a real analogy between these periodic phenomena of growth and the well-known phenomenon of periodic, or oscillatory, chemical change, as described by W. Ostwald and others; cf. (e.g.) *Zeitschr. f. phys. Chem.* xxxv, pp. 33, 204, 1900.

We may want now and then to make use of scanty data, and find a rough estimate better than none. The giant tortoises of the Galapagos and the Seychelles grow to a great age, and some have weighed 500 lb. and more; but the scanty records of captive tortoises shew much variation, depending on food and climate as well as age. Ninety young tortoises brought from the Galapagos in 1928 to the southern United States weighed on the average $18\frac{1}{2}$ lb., and grew to 44·3 lb. in two years. Six taken to Honolulu weighed $26\frac{1}{2}$ lb. each in 1929, and 63 lb. each the following year. Another, kept in California, weighed 29 lb. and 360 lb. seven years later, but only gained 65 lb. more in the next seven years. Growth,

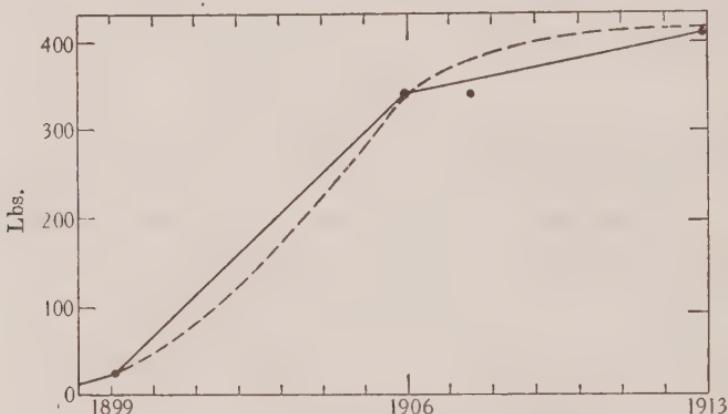


Fig. 41. Approximate growth in weight of Galapagos tortoise.

as usual, is quick to begin with, slower later on, and in the old giants must be slow indeed. If we plot (Fig. 41) the three successive weights of the Californian specimen, at first they help us little; but we can fit an S-shaped curve to the three points as a first approximation, and it suggests, with some plausibility, that, at 29 lb. weight the tortoise was from two to three years old. A loggerhead turtle, which reaches a great size, was found to grow from a few grammes to 42 lb. in three years, and to double that weight in another year and a half; these scanty data are in fair accord, so far as they go, with those for the giant tortoises*.

* For these and other data, see C. H. Townsend, Growth and age in the giant tortoises of the Galapagos, *Zoologica*, ix, pp. 459–466, 1931; G. H. Parker, Growth of the loggerhead turtle, *Amer. Naturalist*, LXVII, pp. 367–373, 1929; Stanley F. Flower, Duration of Life in Animals, III, Reptiles, *D.Z.S. (A)*, 1937, pp. 1–39.

The horny plates of the tortoise grow, to begin with, a trifle faster than the bony carapace below, and are consequently wrinkled into folds. There is some evidence, at least in the young tortoises, that these folds come once a year, which is as much as to say that there is one season of the year when the growth-rates of bony and horny carapace are especially discrepant. This would give an easy estimate of age; but it is plainer in some species than in others, and it never lasts for long.

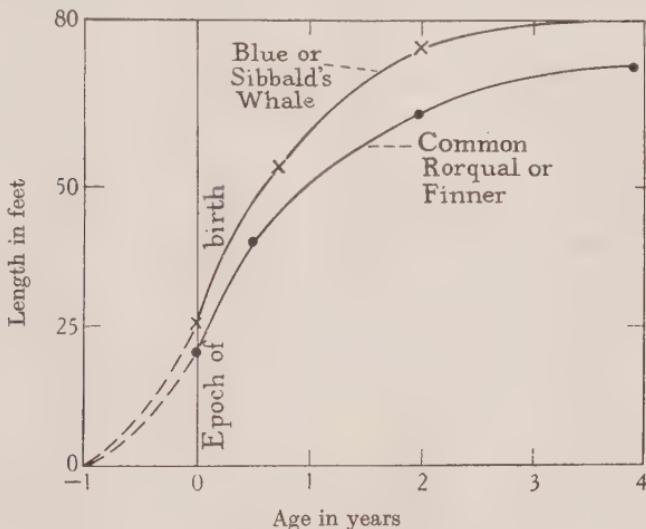


Fig. 42. Growth-rate (approximate) of blue and finner whales.

The blue whale, or Sibbald's rorqual, largest of all animals, grows to 100 ft. long or thereby, the females being a little bigger than the males. The mother goes with young eleven months. The calf measures 22 to 25 ft. at birth, and weighs between three and four tons; it is born big, were it smaller it might lose heat too quickly. It is weaned about nine months later, and is said to be some 16 metres, or say 53 ft., long by then. It is believed to be mature at two years old, by which time it is variously stated to be 60 or even 75 ft. long; the modal size of pregnant females is about 80 ft. or rather more. How long the whale takes to grow the further 15 or 20 feet which bring it to its full size is not known; but, even so far, the rapid growth and early maturity seem very remarkable (Fig. 42). The Norwegian whalers give us statistics,

month by month during the Antarctic season, of the sizes of pregnant females and the foetuses they contain; and from these I draw the following averages:

*Antarctic blue whales; length of mother and of foetus
(Season 1938-39)*

	Number measured	Mother	Foetus
Nov. 1, 1938	59	84.0 ft.	4.2 ft.
16	86	83.0	4.6
Dec. 1	359	84.0	6.1
16	522	83.6	7.0
Jan. 1, 1939	403	83.7	8.4
16	317	84.8	9.3
Feb. 1	184	83.9	11.2
16	125	83.9	12.3
Mar. 1	71	83.6	14.5
	2126	83.8	

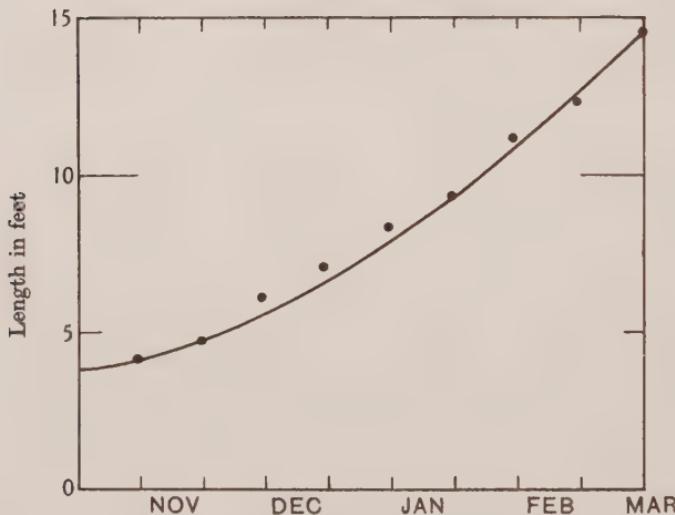


Fig. 43. Pre-natal growth of blue whale. Average monthly sizes, from data in *International Whaling Statistics*, xiv, 1940.

The observations are rough but numerous. At the lower end of the scale measurements are few, and the value indicated is probably too high; but on the whole the curve of growth tallies with other estimates, and points to birth about June or July, and to conception about the same time last year (Fig. 43). The mean size of the mother-whales does not alter during the five months in question;

they do not seem to be increasing, though at 84 ft. they still have another 10 feet or more to grow. They may grow slower, and live longer, than is often supposed*.

On the other hand, if we draw from the same official statistics the mean size of mother-whale and foetus at some given epoch of the year (e.g. March 1934), there appears to be a marked correlation between them, such as would indicate very considerable growth of the mother during the months of pregnancy. The matter deserves further study, and the data need confirmation.

Blue whales; length of mother and foetus (March 1934)

Number observed	Size (ft.)		Size of foetus (ft.) smoothed in threes
	Mother	Foetus	
1	74	1·0	—
1	75	7·0	4·4
5	76	5·2	6·4
7	77	7·3	6·4
9	78	6·7	6·9
10	79	6·7	6·8
21	80	7·1	7·2
27	81	7·7	7·5
28	82	7·6	7·9
33	83	8·4	8·3
38	84	8·9	8·6
46	85	8·5	8·6
37	86	8·5	8·8
19	87	9·5	9·3
18	88	9·9	10·3
12	89	11·4	10·9
18	90	11·5	11·1
9	91	10·4	11·1
2	92	11·5	—

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On the growth of fishes, and the determination of their age

We may keep a child under observation, and weigh and measure him every day; but more roundabout ways are needed to determine the age and growth of the fish in the sea. A few fish may be caught and marked, on the chance of their being caught again; or a few

* The growth of the finner whale, or common rorqual, is estimated as follows (Hamburg Museum): at birth, 6 m.; at 6 months, 12 m.; at one and two years old, 15 and 19 m.; when full-grown, at 6–8 (?) years old, 21 m. For data, see *Hvalradets Skrifter* and *International Whaling Statistics*, *passim*; also N. Mackintosh and others in *Discovery Reports*; also Sigmund Rusting, *Statistics of whales and whale-foetuses, Rapports du Conseil Int.* 1928; etc.

more may be kept in a tank or pond and watched as they grow. Both ways are slow and difficult. The advantage of large numbers is not obtained; and it is needed all the more because the rate of growth turns out to be very variable in fishes, as it doubtless is in all cold-blooded or "poecilothermic" animals: changing and fluctuating not only with age and season, but with food-supply, temperature and other known and unknown conditions. Trout in a chalk-stream so differ from those in the peaty water of a highland burn that the former may grow to three pounds weight while the latter only reach four ounces, at three years old or four*.

It is found (and easily verified) that shells on the seashore, kind for kind, do not follow normal curves of frequency in respect of magnitude, but fall into *size-groups* with intervals between, so constituting a *multimodal curve*. The reason is that they are not born all the year round, as we are, but each at a certain annual breeding-season; so that the whole population consists of so many "groups," each one year older, and bigger in proportion, than another. In short we find *size-groups*, and recognise them as *age-groups*. Each group has its own spread or scatter, which increases with size and age; even from the first one group tends to overlap another, but the older groups do so more and more, for they have had more time and chance to vary. Hence this way of determining age gets harder and less certain as the years go by; but it is a safe and useful method for short-lived animals, or in the early lifetime of the rest. Aristotle's fishermen used it when they recognised three sorts or sizes of tunnies, the auxids, pelamyds and full-grown fish; and when they found a scarcity of pelamyds in one year to be followed by a failure of the tunny-fishery in the next†.

Shells lend themselves to this method, as Louis Agassiz found when he gathered periwinkles on the New England shore. Winckworth found the *Paphiae* in Madras harbour "of two sizes, one group just under 15 mm. in length, the other nearly all over 30 mm. A small sample, dredged five months earlier from the same ground, was intermediate between the other two." When the mean sizes of the two groups were plotted against time, the lesser group being shifted

* Cf. C. A. Wingfield, Effect of environmental factors on the growth of brown trout, *Journ. Exp. Biol.* xvii, pp. 435-448, 1939.

† Aristotle, *Hist. Anim.* vi, 571 a.

back a year, a growth-curve extending over two seasons was obtained; when extrapolated, it seemed to start from zero about May or June, and this date, at the beginning of the hot season, was in all probability the actual spawning time. Growth stopped in winter, a common thing in our northern climate but surprising at Madras, where the sea-temperature seldom falls below 24° C. Shells over 40 mm. long were rare, and over 50 mm. hardly to be found—an indication that *Paphia* seldom lives over a third season. Here then, though the numbers studied were all too few, the method tells us with little doubt or ambiguity the age of a sample and the growth-rate of the species to which it belongs*.

Dr C. J. G. Petersen of Copenhagen brought this method into use for the study of fishes, and up to a certain point it is safe and trustworthy though seldom easy. For one thing, it is hard to get a "random sample" of fish, for one net catches the big and another the small. The trawl-net takes all the big, but lets more and more of the small ones through. The drift-net catches herring by their heads; if too big, the head fails to catch and the fish goes free, if too small the fish slips through; so the net *selects* a certain modal size according to its mesh, and with no great spread or scatter. When we use Petersen's method and plot the sizes of our catch of fish, the younger age-groups are easily recognised, even though they tend to overlap; but the older fish are few, each size-group has a wider spread, and soon the groups merge together and the modal cusps cease to be recognisable. There is no way, save a rough conjectural one, of analysing the composite curve into the several groups of which it is composed; in short, this method works well for the younger, but fails for the older fish.

Fig. 44 is drawn from a catch of some 500 small cod, or codling, caught one November in the Firth of Forth. in a small-meshed experimental trawl-net. They are too few for the law of large numbers to take full effect; but after smoothing the curve, three peaks are clearly seen, with some sign of a fourth, indicating *about*

* R. Winckworth, Growth of *Paphia undulata*, *Proc. Malacolog. Soc.* xix, pp. 171–174, 1931. Cf. (*int. al.*) Weymouth, on *Mactra stultorum*, *Bull. Calif. Fish Comm.* vii, 1923; Orton, on *Cardium*, *Journ. Mar. Biol. Assoc.* xiv, 1927, on *Ostrea*, and on *Patella*, *ibid.* xv, 1928; Ikuso Hamai, on Limpets, *Sci. Rep. Tohoku Imp. Univ.* (4), xii, 1937.

11 cm., 26, 44 and 60 cm., as the mean or modal sizes of four successive broods. The dwindling heights of the successive cusps are a first approximation to a "curve of mortality," shewing how the young are many and the old are few. Again, plotting the several sizes against time, we should get our curve of growth for four years, or a first rough approximation to it. Thus we learn from a random sample, caught in a single haul, the mean (or modal) sizes of a fish at several epochs of its life, say at two, three or even more successive intervals of a year; and we learn (to a first approximation) its rate of growth and its actual age, for the slope of the growth-curve, drawing to the base-line, points to the time when growth began.

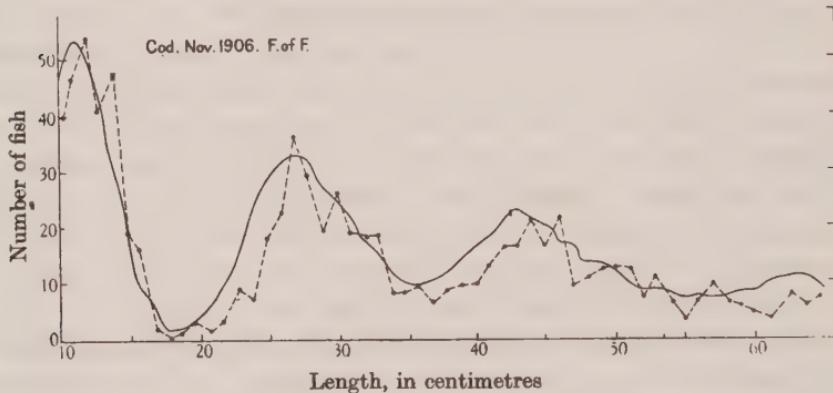


Fig. 44. A catch of cod, shewing a multimodal curve of frequency.

Another haul, soon after, will add new points to the curve, and confirm our first rough approximation.

An experiment in the Moray Firth, a month or two later, shewed the first three annual groups in much the same way; but it also shewed another group, of about 90 cm. long, and others larger still. At first sight these did not seem to fit on to our four successive year-groups, of 11, 26, 44 and 60 cm.; but they did so after all, only *with a gap between*. They were older fish, six and seven years old, which had come back to the Moray Firth to breed after spending a couple of years elsewhere.

It was thought at first that every such experiment should tally with another, and bring us to a more and more accurate knowledge of the growth-rate of this fish or that; but there were continual discrepancies, and it was soon found that the rate varied from place

to place, from month to month, and from one year to another. The growth-rate of a fish varies far more than does that of a warm-blooded animal. The general character of the curve remains*, save that the fish continues to grow even in extreme old age, but it draws towards its upper asymptote with exceeding slowness.

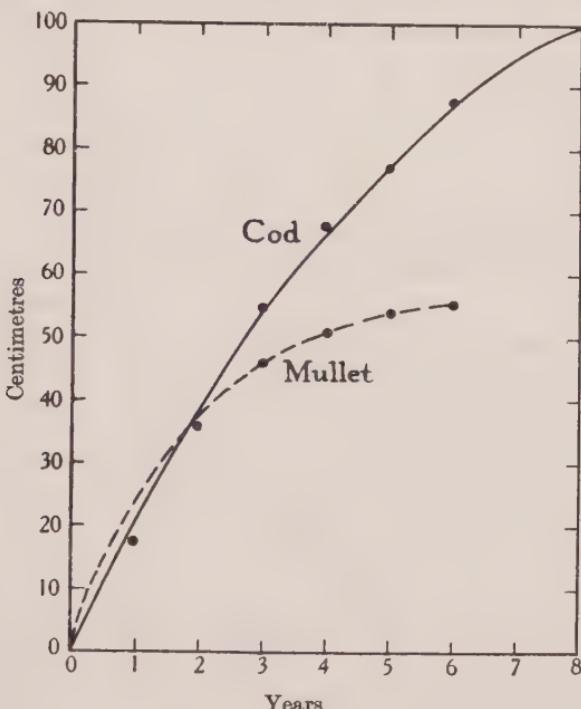


Fig. 45. Growth of cod (after Michael Graham); and of mullet (after C. D. Serbetis).

The following estimate of the mean growth of North Sea cod is based, by Michael Graham, on a great mass of various evidence; and beside it, for comparison, is an estimate for the grey mullet, by C. D. Serbetis. The shape of the curve (Fig. 45) is enough to indicate that at six years old the cod is still growing vigorously†, while the grey mullet has all but ceased to grow. As a matter of

* It is essentially an S-shaped curve, as usual; but the conditions of larval life obscure the first beginnings of the S.

† Norwegian results, based largely on otoliths, are different. Gunner Rollefson holds that the spawning cod, or skrei, do not reach maturity, for the most part, till 10 or 11 years old, and grow by no more than 1 to 3 cms. a year (*Fiskeriskrifter, Bergen*, 1933).

fact, 90 cm. is, or was till lately, the median size of cod* in our Scottish trawl-fishery; one-tenth are over a metre long and the largest are in the neighbourhood of 120 cm., with an occasional giant of 150 cm. or even more. But it has come to pass that fish of outstanding size are seen no more save on the virgin fishing grounds; a Greenland halibut, brought home to Hull in 1938, weighed four hundredweight, was nearly two feet thick, and must have been of prodigious age.

Age (years) ...	1	2	3	4	5	6
Length of cod (cm.)	18	36	55	68	79	89
Length of grey mullet	21	36	46	51	53	55

There are other ways of determining, or estimating, a fish's age. The Greek fishermen shewed Aristotle† how to tell the age of the purple Murex, up to six years old, by counting the whorls and sculptured ridges of the shell, and also how to estimate the age of a scaly fish by the size and hardness of its scales; and Leeuwenhoek saw that a carp's scales‡ bear concentric rings, which increase in number as the fish grows old. In these and other cases, as in the woody rings of a tree, some part of plant or animal carries a record of its own age; and this record may be plain and certain, or may too often be dubious and equivocal.

The scales of most fishes shew concentric rings, sometimes (as in the herring) of a simple kind, sometimes (as in the cod) in a more complex pattern; and the ear-bones, or otoliths, shew opaque concentric zones in their translucent structure. The scales are "read" with apparent ease in herring, haddock, salmon, the otoliths in plaice and hake; but the whole matter is beset with difficulties, and every result deserves to be checked and scrutinised§.

* As distinguished from "codling."

† *Hist. Animalium*, 547b, 10; 607b, 30.

‡ The carp-breeder is especially interested in the age of his fish; for, like the brewer with his yeast, his profit depends on the rate at which they grow. Leeuwenhoek's and other early observations were brought to light by C. Hoffbauer, *Die Alterbestimmung der Karpfen an seiner Schuppen*, *Jahresber. d. schles. Fischerei-Vereins*, Breslau, 1899.

§ Thus, for instance, Mr A. Dannevig says (On the age and growth of the cod, *Fiskeridirektorets Skrifter*, 1933, p. 82): "as to the problem of the determination of the age of the cod by means of scales and otoliths, all workers agree that the method is useful. But on a number of fundamental points there are just as many divergences of opinion as there are investigators."

In the following table, we see (*a*) the sizes, and (*b*) the number of scale-rings, in a sample of some 550 herring from the autumn fishery off the east of Scotland.

Rings cm.	3	4	5	6	7	8	9	10	11	12	Total	Mean rings
31	—	—	—	1	1	—	1	—	—	1	4	8.5
30	—	—	—	7	5	6	4	—	—	—	22	7.3
29	—	—	5	18	13	6	6	1	1	1	51	7.0
28	—	3	29	38	11	3	3	1	—	—	88	5.9
27	2	13	41	34	5	5	2	—	—	—	102	5.1
26	7	43	64	29	—	—	1	—	—	—	144	5.0
25	4	36	41	11	—	—	—	—	—	—	92	4.6
24	2	17	15	4	—	—	—	—	—	—	38	4.8
23	—	5	—	—	—	—	—	—	—	—	5	4.0
Total	15	117	195	142	35	20	17	2	1	2	—	—
Mean size	25.6	25.4	26.5	27.4	28.6	28.7	28.8	28.5	—	—	—	—

In this sample, the sizes of the 550 fish are grouped in a somewhat skew curve, about a mode at 26 cm.; and the numbers of scale-rings group themselves in like manner, but with rather more skewness, about a modal number of five rings. Either way we look at it, there is only one "group" of fish; and it is highly characteristic of the herring that a single sample, taken from a single shoal, exhibits a unimodal curve. Accepting in principle the view that scale-rings tend to synchronise with age in years, we may draw this first deduction that our sample consists in part (if not in whole) of five-year old fish, whose average length is about 26 cm.; and this length, of 26 cm. for 5-ringed, or 5-year-old herring, agrees well with many other determinations from the same region. We shall be on the safe side if we deal, after this fashion, with *the one predominant group*, or mode, in each sample of fish; and Fig. 46 shews an approximate curve of growth for our East Coast herring drawn in this way.

But the further assumption is commonly and all but universally made that *each individual herring* carries the record of its age on its scale-rings. If this be so, then our sample of 550 fish is a composite population of some ten separate broods or successive ages, all mixed up in a shoal. And again, if so, the 5-year-olds in the said population average 26.5 cm. in length, the 3-year-olds 25.6 cm., the 10-year-olds 28.5 cm.; but these values do not fit into a normal

curve of growth by any means. Still more obvious is it that the several year-classes (if such they be) do not tally with the age-composition of any ordinary population, nor agree with any ordinary curve of mortality. But even if we had ten separate year-groups represented here, which I most gravely doubt, all that we know of the selective action of the drift-net forbids us to assume that we are dealing with a fair random sample of the herring population; so that, even though the number of rings did enable us to distinguish the successive broods, we should still have no right to assume that

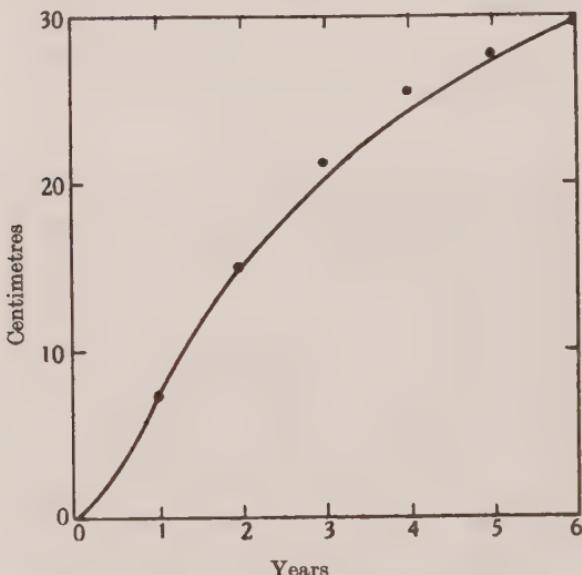


Fig. 46. Mean curve of growth of Scottish (East Coast) herring.

these annual broods actually combine in the proportions shewn, to form the composite population.

It is held by many (in the first instance by Einar Lea) that we may deduce the dimensions of a herring at each stage of its past life from the corresponding dimensions of the rings upon its scales. Some such relation must obviously exist, but it is an approximation of the roughest kind. For it involves the assumption not only that the scales add ring to ring regularly year to year, and that fish and scale grow all the while at corresponding rates or in direct proportion to one another, but also that the scale grows by mere

accretion, each annual increment persisting without further change after it is once laid down. This is what happens in a molluscan shell, which is secreted or deposited as mere dead substance or "formed material"; but it is by no means the case in bone, and we have little reason to expect it of the bony mesoblastic tissue of a fish's scale. It is much more likely (though we do not know for sure) that "osteoblasts" and "osteoclasts" continue (as in bone) to play their part in the scale's growth and maintenance, and that some sort of give and take goes on. In any case, it is a matter of

*Mean apparent length of one-year-old herring, as deduced by scale-reading from herring of various ages or "year-classes"**

Year-class (or number of rings)	2	3	4	5	6	7	8	9
Estimated length at 1 year old	14.5	13.2	12.7	12.5	12.1	11.8	11.9	11.8

fact and observation that the rings alter in breadth as the fish goes on growing †; that the oldest or innermost rings grow steadily narrower, while the outermost hardly change or even widen a little; that the relative breadths of successive rings alter accordingly; and it follows that when we try to trace the growth of a herring through its lifetime from its scales when it is old, the result is more or less misleading, and the values for the earlier years are apt to be much too small. The whole subject is very difficult, as we might well expect it to be; and I am only concerned to shew some small part of its difficulty ‡.

While careful observations on the rate of growth of the higher animals are scanty, they shew so far as they go that the general features of the phenomenon are much the same. Whether the animal be long-lived, as man or elephant, or short-lived like horse §

* From T. Emrys Watkin, *The Drift Herring of the S.E. of Ireland, Rapports du Conseil pour l'Exploration de la Mer*, LXXXIV, p. 85, 1933.

† Cf. (*int. al.*) Rosa M. Lee, *Methods of age and growth determination in fishes by means of scales, Fishery Investigations, Dept. of Agr. and Fisheries*, 1920.

‡ The copious literature of the subject is epitomised, so far, by Michael Graham, in *Fishery Investigations* (2), xi, No. 3, 1928.

§ There is a famous passage in Lucretius (v, 883) where he compares the course of life, or rate of growth, in the horse and his boyish master: *Principio circum tribus actis impiger annis Floret equus, puer hautquaquam*, etc.

or dog, it passes through the same phases of growth; and, to quote Dr Johnson again, "whatsoever is formed for long duration arrives slowly to its maturity*." In all cases growth begins slowly; it attains a maximum velocity somewhat early in its course, and afterwards slows down (subject to temporary accelerations) towards a point where growth ceases altogether. But in cold-blooded animals, as fish or tortoises, the slowing down is greatly protracted, and the size of the creature would seem never to reach, but only to approach asymptotically, to a maximal limit. This, after all, is an important difference. Among certain still lower animals growth ceases early but life goes on, and draws (apparently) to no predetermined end. So sea-anemones have been kept in captivity for sixty or even eighty years, have fed, flourished and borne offspring all the while, but have shewn no growth at all.

The rate of growth of various parts or organs†

That the several parts and organs of the body, within and without, have their own rates of growth can be amply demonstrated in the case of man, and illustrated also, but chiefly in regard to external form, in other animals. There lies herein an endless field for the study of correlation and of variability‡.

In the accompanying table I show, from some of Vierordt's data, the relative weights at various ages, compared with the weight at birth, of the entire body, and of brain, heart and liver; also the changing relation which each of these organs consequently bears, as time goes on, to the weight of the whole body (Fig. 47)§.

* All of which is tantamount to a mere change of scale of the time-curve.

† This phenomenon, of *incrementum inequale*, as opposed to *incrementum in universum*, was most carefully studied by Haller: "Incrementum inequale multis modis fit, ut aliae partes corporis aliis celerius increscant. Diximus hepar minus fieri, majorem pulmonem, minimum thymum, etc." (*Elem.* VIII (2), p. 34.)

‡ See (*int. al.*) A. Fischel, Variabilität und Wachsthum des embryonalen Körpers, *Morphol. Jahrb.* xxiv, pp. 369–404, 1896; Oppel, *Vergleichung des Entwickelungsgrades der Organe zu verschiedenen Entwickelungszeiten bei Wirbeltieren*, Jena, 1891; C. M. Jackson, Pre-natal growth of the human body and the relative growth of the various organs and parts, *Amer. Journ. of Anat.* ix, 1909; and of the albino rat, *ibid.* xv, 1913; L. A. Calkins, Growth of the human body in the foetal period, *Rep. Amer. Assoc. Anat.* 1921. For still more detailed measurements, see A. Arnold, Körperuntersuchungen an 1656 Leipziger Studenten, *Ztschr. f. Konstitutionslehre*, xv, pp. 43–113, 1929.

§ From Vierordt's *Anatomische Tabellen*, pp. 38, 3rd, much abbreviated.

Weight of various organs, compared with the total weight of the human body (male). (From Vierordt's Anatomische Tabellen)

Age	Wt. (kgm.)	Percentage increase				Percentage of body-wt.		
		Body	Brain	Heart	Liver	Brain	Heart	Liver
0	3.1	1.0	1.0	1.0	1.0	12.3	0.76	4.6
1	9.0	2.9	2.5	1.8	2.4	10.5	0.46	3.7
2	11.0	3.6	2.7	2.2	3.0	9.3	0.47	3.9
3	12.5	4.0	2.9	2.8	3.4	8.9	0.52	3.9
4	14.0	4.5	3.5	3.1	4.2	9.5	0.53	4.2
5	15.9	5.1	3.3	3.9	3.8	7.9	0.51	3.4
6	17.8	5.7	3.6	3.6	4.3	7.6	0.48	3.5
7	19.7	6.4	3.5	3.9	4.9	6.8	0.47	3.5
8	21.6	7.0	3.6	4.0	4.6	6.4	0.44	3.0
9	23.5	7.6	3.7	4.6	5.0	6.1	0.46	3.0
10	25.2	8.1	3.7	5.4	5.9	5.6	0.51	3.3
11	27.0	8.7	3.6	6.0	6.1	5.0	0.52	3.2
12	29.0	9.4	3.8	(4.1)	6.2	4.9	(0.34)	3.0
13	33.1	10.7	3.9	7.0	7.3	4.5	0.50	3.1
14	37.1	12.0	3.4	9.2	8.4	3.5	0.58	3.2
15	41.2	13.3	3.9	8.5	9.2	3.6	0.48	3.2
16	45.9	14.8	3.8	9.8	9.5	3.2	0.51	3.0
17	49.7	16.0	3.7	10.6	10.5	2.8	0.51	3.0
18	53.9	17.4	3.7	10.3	10.7	2.6	0.46	2.8
19	57.6	18.6	3.7	11.4	11.6	2.4	0.51	2.9
20	59.5	19.2	3.8	12.9	11.0	2.4	0.51	2.6
21	61.2	19.7	3.7	12.5	11.5	2.3	0.49	2.7
22	62.9	20.3	3.5	13.2	11.8	2.2	0.50	2.7
23	64.5	20.8	3.6	12.4	10.8	2.2	0.46	2.4
24	—	—	3.7	13.1	13.0	—	—	—
25	66.2	21.4	3.8	12.7	12.8	2.2	0.46	2.8

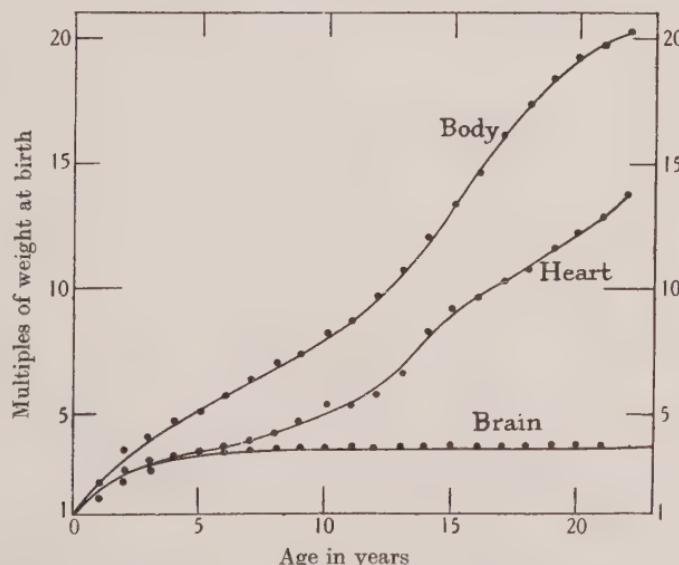


Fig. 47. Relative growth in weight of brain, heart and body of man.
From Quetelet's data (smoothed curves).

We see that neither brain, heart nor liver keeps pace by any means with the growing weight of the whole; there must then be other parts of the fabric, probably the muscles and the bones, which increase *more* rapidly than the general average. Heart and liver grow nearly at the same rate, the liver keeping a little ahead to begin with, and the heart making up on it in the end; by the age of twenty-five both have multiplied their original weight at birth about thirteen times, but the body as a whole has multiplied by twenty-one. In contrast to these the brain has only multiplied its weight about three and three-quarter times, and shews but little increase since the child was four or five, and hardly any since it was eight years old. Man and the gorilla are born with brains much of a size; but the gorilla's brain stops growing very soon indeed, while the child's has four years of steady increase. The child's brain grows quicker than the gorilla's, but the great ape's body grows much quicker than the child's; at four years old the young gorilla has reached about 80 per cent. of his bodily stature, and the child's brain has reached about 80 per cent. of its full size.

Even during foetal life, as well as afterwards, the *relative* weight of the brain keeps on declining. It is about 18 per cent. of the body-weight in the third month, 16 per cent. in the fourth, 14 per cent. in the fifth; and the ratio falls slowly till it comes to about 12 per cent. at birth, say 10 per cent. a year afterwards, and little more than 2 per cent. at twenty*. Many statistics indicate a further decrease of brain-weight, actual as well as relative. The fact has been doubted and denied; but Raymond Pearl has shewn evidence of a slow decline continuing throughout adult life†.

The latter part of the table shews the decreasing weights of the organs compared with the body as a whole: brain, which was 12 per cent. of the body-weight at birth, falling to 2 per cent. at five-and-twenty; heart from 0·76 to 0·46 per cent.; liver from 4·6 to 2·78 per cent. The thyroid gland (as we know it in the rat) grows for a few weeks, and then diminishes during all the rest of the creature's lifetime; even during the brief period of its own growth it is growing slower than the body as a whole.

It is plain, then, that there is no simple and direct relation, holding

* Cf. J. Ariens Kappers, *Proc. K. Akad. Wetensch., Amsterdam*, xxxix, No. 7, 1936.

† R. Pearl, Variation and correlation in brain-weight, *Biometrika*, iv, pp. 13–104, 1905.

good throughout life, between the size of the body and its organs; and the ratio of magnitude tends to change not only as the individual grows, but also with change of bodily size from one individual, one race, one species to another. In giant and pygmy breeds of rabbits, the organs have by no means the same ratio to the body-weight; but if we choose individuals of the same weight, then the ratios tend to be identical, irrespective of breed*. The larger breeds of dogs are for the most part lighter and slenderer than the small, and the organs change their proportions with their size. The spleen keeps pace with the weight of the body; but the liver, like the brain, becomes relatively less. It falls from about 6 per cent. of the body-weight in little dogs to rather over 2 per cent. in a great hound†.

The changing ratio with increasing magnitude is especially marked in the case of the brain, which constitutes (as we have just seen) an eighth of the body-weight at birth, and but one-fiftieth at twenty-five. This falling ratio finds its parallel in comparative anatomy, in the general law that the larger the animal the smaller (relatively) is the brain‡. A falling ratio of brain-weight during life is seen in other animals. Max Weber§ tells us that in the lion, at five weeks, four months, eleven months and lastly when full-grown, the brain represents the following fractions of the weight of the body: viz. $1/18$, $1/80$, $1/184$ and $1/546$. And Kellicott has shewn that in the dogfish, while certain organs, e.g. pancreas and rectal gland, grow *pari passu* with the body, the brain grows in a diminishing ratio, to be represented (roughly) by a logarithmic curve||.

In the grown man, Raymond Pearl has shewn brain weight to increase with the stature of the individual and to decrease with his age, both in a straight-line ratio, or *linear regression*, as the

* R. C. Robb, Hereditary size-limitation in the rabbit, *Journ. Exp. Biol.* vi, 1929.

† Cf. H. Vorsteher, *Einfluss d. Gesamtgrösse auf die Zusammensetzung des Körpers*; Diss., Leipzig, 1923.

‡ Oliver Goldsmith argues in his *Animated Nature* as follows, regarding the unlikeness of dwarfs or giants: "Had man been born a dwarf, he could not have been a reasonable creature; for to that end, he must have a jolt head, and then he would not have body and blood enough to supply his brain with spirits; or if he had a small head, proportionable to his body, there would not be brain enough for conducting life. But it is still worse with giants, etc."

§ *Die Säugetiere*, p. 117.

|| *Amer. Journ. of Anatomy*, viii, pp. 319-353, 1908.

statisticians call it. Thus the following wholly empirical equations give the required ratios in the case of Swedish males:

$$\begin{aligned}\text{Brain-weight (gms.)} &= 1487.8 - 1.94 \times \text{age, or} \\ &= 915.06 + 2.86 \times \text{stature.}\end{aligned}$$

In the two sexes, and in different races, these empirical constants will be greatly changed*; and Donaldson has further shewn that correlation between brain-weight and body-weight is much closer in the rat than in man†.

	Weight of entire animal (gm.) <i>W</i>	Weight of brain (gm.) <i>w</i>	Ratios	In <i>wⁿ = W</i>
Marmoset	335	12.5	$1: 26$	$1: 2.0$
Spider monkey	1,845	126	15	1.1
<i>Felis minuta</i>	1,234	23.6	52	1.2
<i>F. domestica</i>	3,300	31	107	2.4
Leopard	27,700	164	168	1.2
Lion	119,500	219	546	1.3
Dik-dik	4,575	37	124	2.7
Steinbok	8,600	49.5	173	2.9
Impala	37,900	148.5	255	2.75
Wildebeest	212,200	443	479	2.8
Zebra	255,000	541	472	2.7
"	297,000	555	536	2.8
Rhinoceros	765,000	655	1170	3.6
Elephant	3,048,000	5,430	560	2.0
Whale (<i>Globiocephalus</i>)	1,000,000	2,511	400	2.0
			Mean	2.23
				2.06

Brandt, a very philosophical anatomist, argued some seventy years ago that the brain, being essentially a hollow structure, a surface rather than a mass, ought to be equated with the surface rather than the mass of the animal. This we may do by taking the square-root of the brain-weight and the cube-root of the body-weight; and while the ratios so obtained do not point to *equality*, they do tend to *constancy*, especially if we limit our comparison to similar or related animals. Or we may vary the method, and ask (as Dubois has done) to what power the brain-weight must be raised

* *Biometrika*, iv, pp. 13-105, 1904.

† H. H. Donaldson, A comparison of the white rat with man, etc., *Boas Memorial Volume*, New York, 1906, pp. 5-26.

to equal the body-weight; and here again we find the same tendency towards uniformity*.

The converse to the unequal growth of organs is found in their unequal loss of weight under starvation. Chossat found, in a well-known experiment, that a starved pigeon had lost 93 per cent. of its fat, about 70 per cent. of liver and spleen, 40 per cent. of its muscles, and only 2 per cent. of brain and nervous tissues†. The salmon spends many weeks in the river before spawning, without taking food. The muscles waste enormously, but the reproductive bodies continue to grow.

As the internal organs of the body grow at different rates, so that their ratios one to another alter as time goes on, so is it with those linear dimensions whose inconstant ratios constitute the changing form and proportions of the body. In one of Quetelet's tables he shews the span of the outstretched arms from year to year, compared with the vertical stature. It happens that height and span are so nearly co-equal in man that direct comparison means little; but the *ratio* of span to height (Fig. 48) undergoes a significant and remarkable change. The man grows faster in stretch of arms than he does in height, and span which was less at birth than stature by about 1 per cent. exceeds it by about 4 per cent. at the age of twenty. Quetelet's data are few for later years, but it is clear enough that span goes on increasing in proportion to stature. How far this is due to actual growth of the arms and how far to increasing breadth of the chest is another story, and is not yet ascertained.

* Cf. A. Brandt, Sur le rapport du poids du cerveau à celui du corps chez différents animaux, *Bull. de la Soc. Imp. des naturalistes de Moscou*, XL, p. 525, 1867; J. Baillanger, De l'étendu de la surface du cerveau, *Ann. Med. Psychol.* xvii, p. 1, 1853; Th. van Bischoff, *Das Hirngewicht des Menschen*, Bonn, 1880 (170 pp.), cf. *Biol. Centralbl.* I, pp. 531–541, 1881; E. Dubois, On the relation between the quantity of brain and the size of the body, *Proc. K. Akad. Wetensch., Amsterdam*, xvi, 1913. Also, Th. Ziehen, *Maszverhältnisse des Gehirns*, in Bardeleben's *Handb. d. Anatomie des Menschen*; P. Warneke, *Gehirn u. Körpergewichtsbestimmungen bei Säugern*, *Journ. f. Psychol. u. Neurol.* xiii, pp. 355–403, 1909; B. Klatt, Studien zum Domestikationsproblem, *Bibliotheca genetica*, II, 1921; etc. The case of the heart is somewhat analogous; see Parrot, *Zool. Jahrb. (System.)*, vii, 1894; Platt, in *Biol. Centralbl.* xxxix, p. 406, 1919.

† C. Chossat, Recherches sur l'inanition, *Mém. Acad. des Sci., Paris*, 1843, p. 438.

The growth-rates of head and body differ still more; for the height of the head is no more than doubled, but stature is trebled,

*Height of the head in man at various ages**
(After Quetelet, p. 207, abbreviated)

Age	Men			Women			Ratio
	Stature m.	Head m.	Ratio	Stature m.	Head m.		
Birth	0.50	0.11	4.5	0.49	0.11		4.4
1 year	0.70	0.15	4.5	0.69	0.15		4.5
2 years	0.79	0.17	4.6	0.78	0.17		4.5
3 "	0.86	0.18	4.7	0.85	0.18		4.7
5 "	0.99	0.19	5.1	0.97	0.19		5.1
10 "	1.27	0.21	6.2	1.25	0.20		6.2
20 "	1.51	0.22	7.0	1.49	0.21		7.0
25 "	1.67	0.23	7.3	1.57	0.22		7.1
30 "	1.69	0.23	7.4	1.58	0.22		7.1
40 "	1.69	0.23	7.4	1.58	0.22		7.1

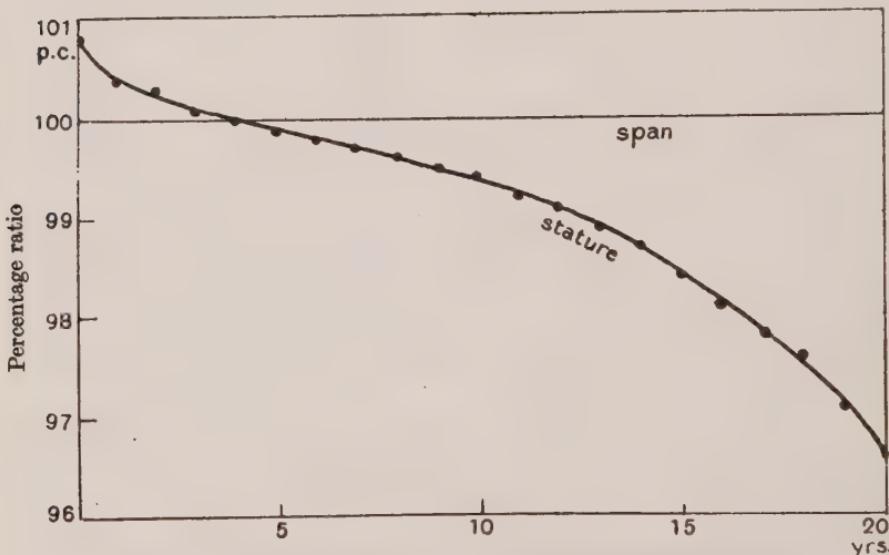


Fig. 48. Ratio of stature in man, to span of outstretched arms.
From Quetelet's data.

between infancy and manhood. Dürer studied and illustrated this remarkable phenomenon, and the difference which accompanies and

* A smooth curve, very similar to this, is given by Karl Pearson for the growth in "auricular height" of the girl's head, in *Biometrika*, III, p. 141, 1904.

results from it in the bodily form of the child and the man is easy to see.

The following table shews the relative sizes of certain parts and organs of a young trout during its most rapid development; and so illustrates in a simple way the varying growth-rates in different parts of the body*. It would not be difficult, from a picture of the little trout at any one of these stages, to draw its approximate form at any other by the help of the numerical data here set forth. In like manner a herring's head and tail grow longer, the parts between grow relatively less, and the fins change their places a little; the same changes take place with their specific differences in related fishes, and herring, sprat and pilchard owe their specific characters to their rates of growth or modes of increment†.

*Trout (Salmo fario): proportionate growth of various organs
(From Jenkinson's data)*

Days old	Total length	Eye	Head	1st dorsal	Ventral fin	2nd dorsal	Tail fin	Breadth of tail
40	100	100	100	100	100	100	100	100
63	130	129	148	149	149	108	174	156
77	155	147	189	(204)	(194)	139	258	220
92	173	179	220	(193)	(182)	155	308	272
106	195	193	243	173	165	173	337	288

Sachs studied the same phenomenon in plants, after a method in use by Stephen Hales a hundred and fifty years before. On the growing root of a bean ten narrow zones were marked off, starting from the apex, each zone a millimetre long. After twenty-four hours' growth (at a given temperature) the whole ten zones had grown from 10 to 33 mm., but the several zones had grown very unequally, as shewn in the annexed table‡ (p. 192):

* Cf. J. W. Jenkinson, Growth, variability and correlation in young trout, *Biometrika*, viii, pp. 444–466, 1912.

† Cf. E. Ford, On the transition from larval to adolescent herring, *Journ. Mar. Biol. Assoc.* xvi, p. 723; xviii, p. 977, 1930–31. So also in larval eels, tail and body grow at different rates, which rates differ in different species; cf. Johannes Schmidt, *Meddel. Kommiss. Havsundersok.* 1916; L. Bertin, *Bull. Zool. France*, 1926, p. 327.

‡ From Sachs's *Textbook of Botany*, 1882, p. 820.

Graded growth of bean-root

Zone	Increment mm.	Zone	Increment mm.
Apex	1.5	6th	1.3
2nd	5.8	7th	0.5
3rd	8.2	8th	0.3
4th	3.5	9th	0.2
5th	1.6	10th	0.1

"...I marked in the same manner as the Vine, young Honeysuckle shoots, etc....; and I found in them all a gradual scale of unequal extensions, those parts extending most which were tenderest," *Vegetable Staticks*, Exp. cxxiii.

The lengths attained by the successive zones lie very nearly on a smooth curve or gradient; for a certain law, or principle of continuity, connects and governs the growth-rates along the growing axis. This curve has its family likeness to those differential

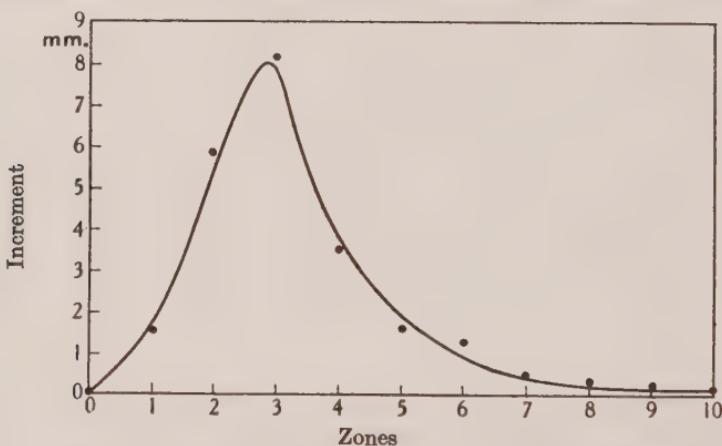


Fig. 49. Rate of growth of bean-root, in successive zones of 1 mm. each, beginning at the tip.

curves which we have already studied, in which rate of growth was plotted against time, as here it is plotted against successive spatial intervals of a growing structure; and its *general* features are those of a curve, a skew curve, of error. Had the several growth-rates been transverse to the axis, instead of being longitudinal and parallel to it, they would have given us a leaf-shaped structure, of which our curve would represent the outline on either side; or again, if growth had been symmetrical about the axis, it might have given us a turnip-shaped solid of revolution. There is always an easy passage from growth to form.

A like problem occurs when we deal with rates of growth in successive natural internodes; and we may then pass from the actual growth of the internodes to the varying number of leaves which they successively produce. Where we have whorls of leaves at each node, as in *Equisetum* or in many water-weeds, then the problem is simplified; and one such case has been studied by Raymond Pearl*. In *Ceratophyllum* the mean number of leaves increases with each successive whorl, but the rate of increase diminishes from whorl to whorl as we ascend. On the main stem the rate of change is very slow; but in the small twigs, or tertiary branches, it becomes rapid, as we see from the following abbreviated table:

*Number of leaves per whorl on the tertiary branches of
Ceratophyllum*

Order of whorl ...	1	2	3	4	5	6
Mean no. of leaves	6.55	8.07	9.00	9.20	9.75	10.00
Smoothed no.	6.5	8.0	9.0	9.5	9.8	10.0

Raymond Pearl gives a logarithmic formula to fit the case; but the main point is that the numbers form a *graded series*, and can be plotted as a simple curve.

In short, a large part of the morphology of the organism depends on the fact that there is not only an average, or aggregate, rate of growth common to the whole, but also a *gradation* of rate from one part to another, tending towards a specific rate characteristic of each part or organ. The least change in the ratio, one to another, of these partial or localised rates of growth will soon be manifested in more and more striking differences of form; and this is as much as to say that the time-element, which is implicit in the idea of *growth*, can never (or very seldom) be wholly neglected in our consideration of form†.

A flowering spray of Montbretia or lily-of-the-valley exemplifies a growth-gradient, after a simple fashion of its own. Along the

* On variation and differentiation in *Ceratophyllum*, *Carnegie Inst. Publications*, No. 58, 1907; see p. 87.

† Herein lies the easy answer to a contention raised by Bergson, and to which he ascribes much importance, that "a mere variation of size is one thing, and a change of form is another." Thus he considers "a change in the form of leaves" to constitute "a profound morphological difference" (*Creative Evolution*, p. 71).

stalk the growth-rate falls away; the florets are of descending age, from flower to bud: their graded differences of age lead to an exquisite gradation of size and form; the time-interval between one and another, or the “space-time relation” between them all, gives a peculiar quality—we may call it phase-beauty—to the whole. A clump of reeds or rushes shews this same phase-beauty, and so do the waves on a cornfield or on the sea. A jet of water is not much, but a fountain becomes a beautiful thing, and the play of many fountains is an enchantment at Versailles.

On the weight-length coefficient, or ponderal index

So much for the visible changes of form which accompany advancing age, and are brought about by a diversity of rates of growth at successive points or in different directions. But it often happens that an animal's change of form may be so gradual as to pass unnoticed, and even careful measurement of such small changes becomes difficult and uncertain. Sometimes one dimension is easily determined, but others are hard to measure with the same accuracy. The length of a fish is easily measured; but the breadth and depth of plaice or haddock are vaguer and more uncertain. We may then make use of that ratio of weight to length which we spoke of in the last chapter: viz. that $W \propto L^3$, or $W = kL^3$, or $W/L^3 = k$, where k , the “ponderal index,” is a constant to be determined for each particular case*.

We speak of this k as a “constant,” with a mean value specific to each species of animal and dependent on the bodily proportions or form of that animal; yet inasmuch as the animal is continually apt to change its bodily proportions during life, k also is continually subject to change, and is indeed a very delicate index of such

* This relation, and how important it is, were clearly recognised by Herbert Spencer in his *Recent Discussions in Science, etc.*, 1871. The formula has been often, and often independently, employed: first perhaps in the form $\frac{\sqrt[3]{W}}{L} \times 100$, by R. Livi, L'indice ponderale, o rapporto tra la statura e il peso, *Atti Soc. Romana Antropologica*, v, 1897. Values of k for man and many animals are given by H. Przibram, in *Form und Formel*, 1922. On its use as an index to the condition or habit of body of an individual, see von Rhode, in Abderhalden's *Arbeitsmethoden*, ix, 4. The constant k might be called, more strictly, k_l , leaving k_b and k_d for the similar constants to be derived from the *breadth* and *depth* of the fish.

progressive changes: delicate—because our measurements of length are very accurate on the whole, and weighing is a still more delicate method of comparison.

Thus, in the case of plaice, when we deal with mean values for large numbers and with samples so far "homogeneous" that they are taken at one place and time, we find that k is by no means constant, but varies, and varies in an orderly way, with increasing size of the fish. The phenomenon is unexpectedly complex, much more so than I was aware of when I first wrote this book. Fig. 50

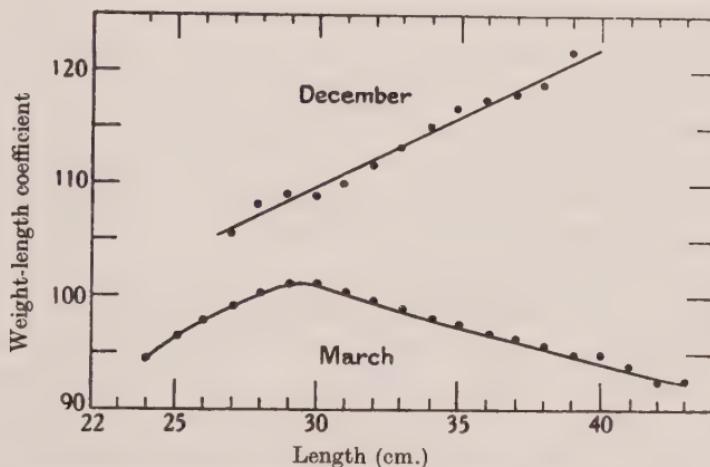


Fig. 50. Changes in the weight-length coefficient of plaice with increasing size; from March and December samples.

shews the weight-length coefficient, or ponderal index, in two large samples, one taken in the month of March, the other in December. In the latter sample k increases steadily as the plaice grow from about 25 to 40 cm. long; weight, that is to say, increases more rapidly than the cube of the length, and it follows that length itself is increasing less rapidly than some other linear dimension. In other words, the plaice grow thicker, or bulkier, with length and age. The other sample, taken in the month of March, is curiously different; for now k rises to a maximum when the fish are somewhere about 30 cm. long, and then declines slowly with further increase in size of the fish; and k itself is less in March than in December, the discrepancy being slight in the small fish and great in the large. The "point of inflection" at 30 cm. or thereby marks

an epoch in the fish's life; it is about the size when sexual maturity begins, or at least near enough to suggest a connection between the two phenomena*.

A step towards further investigation would be to determine k for the two sexes separately, and to see whether or no the point of inflection occurs, as maturity is known to be reached, at a smaller size in the male. This d'Ancona has done, not for the plaice but for the shad (*Alosa finta*). He finds that the males are the first to reach maturity, first to shew a retardation of the rate of growth, first to reach a maximal value of the ponderal index, and in all probability the first to die†.

Again we may enquire whether, or how, k varies with the time of year; and this correlation leads to a striking result‡. For the ponderal index fluctuates periodically with the seasons, falling steeply to a minimum in March or April, and rising slowly to an annual maximum in December (Fig. 51)§. The main and obvious explanation lies in the process of spawning, the rapid loss of weight thereby, and the slow subsequent rebuilding of the reproductive tissues; whence it follows that, without ever seeing the fish spawn, and without ever dissecting one to see the state of its reproductive system, we may by this statistical method ascertain its spawning season, and determine the beginning and end thereof with considerable accuracy. But all the while a similar fluctuation, of much less amplitude, is to be found in young plaice before the spawning age; whence we learn that the fluctuation is not only due to shedding and replacement of spawn, but in part also to seasonal changes in appetite and general condition.

Returning to our former instance, we now see that the March and December samples of plaice, which shewed such discrepant variations of the ponderal index with increasing size, happen to

* The carp shews still more striking changes than does the plaice in the weight-length coefficient: in other words, still greater changes in bodily shape with advancing age and increasing size; cf. P. H. Struthers, *The Champlain Watershed*, Albany, New York, 1930.

† U. d'Ancona, Il problema dell' accrescimento dei pesci, etc., *Mem. R. Acad. dei Lincei* (6), II, pp. 497-540, 1928.

‡ Cf. Lämmel, Ueber periodische Variationen in Organismen, *Biol. Centralbl.* xxii, pp. 368-376, 1903.

§ When we restrict ourselves, for simplicity's sake, to fish of one particular size, we need not determine the values of k , for changes in weight are obvious enough; but when we have small numbers and various sizes to deal with, the determination of k helps very much.

coincide with the beginning and end of the spawning season; the fish were full of spawn in December, but spent and lean in March. The weight-length ratio was, of necessity, higher at the former season; and the falling-off in condition, and in bulk, which the March sample indicates, is more and more pronounced in the larger and therefore more heavily spawn-laden fish.

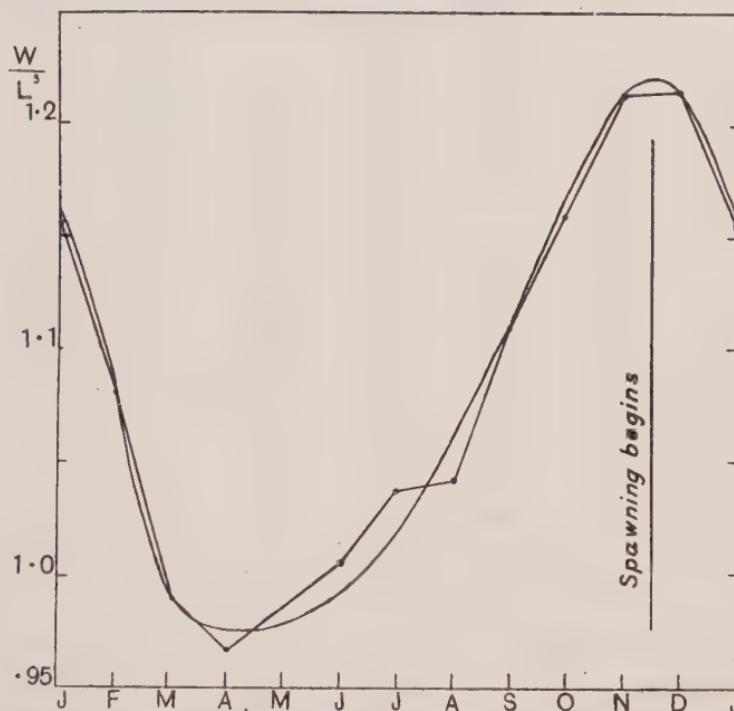


Fig. 51. Periodic annual change in the weight-length ratio of plaice.

Periodic relation of weight to length in plaice of 55 cm. long

	Average weight decigrams	W/L^3	W/L^3 (smoothed)
Jan.	204	1.23	1.16
Feb.	174	1.04	1.08
March	162	0.97	0.99
April	159	0.95	0.97
May	162	0.98	0.98
June	171	1.03	1.01
July	169	1.01	1.04
August	178	1.07	1.04
Sept.	173	1.04	1.11
Oct.	203	1.22	1.16
Nov.	203	1.22	1.21
Dec.	200	1.20	1.22
Mean	180	1.08	

*Plaice caught in a certain area, March 1907 and December 1905.
Variation of k, the weight-length coefficient, with size*

cm.	gm.	March sample		December sample		Do. smoothed
		W/L^3	Do. smoothed	gm.	W/L^3	
23	113	0.93	—	—	—	—
24	128	0.93	0.94	—	—	—
25	152	0.97	0.96	—	—	—
26	178	0.96	0.98	177	1.01	—
27	193	0.98	0.99	209	1.06	1.06
28	221	1.01	1.00	241	1.10	1.08
29	250	1.02	1.01	264	1.08	1.09
30	271	1.00	1.01	294	1.09	1.09
31	300	1.01	1.00	325	1.09	1.10
32	328	1.00	1.00	366	1.12	1.12
33	354	0.99	0.99	410	1.14	1.13
34	384	0.98	0.98	449	1.14	1.15
35	419	0.98	0.98	501	1.17	1.17
36	454	0.97	0.97	556	1.19	1.17
37	492	0.95	0.96	589	1.16	1.18
38	529	0.96	0.96	652	1.19	1.19
39	564	0.95	0.95	719	1.21	1.22
40	614	0.96	0.95	809	1.26	—
41	647	0.94	0.94	—	—	—
42	679	0.92	0.93	—	—	—
43	732	0.92	0.93	—	—	—
44	800	0.94	0.94	—	—	—
45	875	0.96	—	—	—	—

These weights and measurements of plaice are taken from the Department of Agriculture and Fisheries' *Plaice-Report*, I, pp. 65, 107, 1908; II, p. 92, 1909.

Japanese goldfish* are exposed to a much wider range of temperature than our plaice are called on to endure; they hibernate in winter and feed greedily in the heat of summer. Their weight is low in winter but rises in early spring, it falls as low as ever at the height of the spawning season in the month of May; so for one weight-length fluctuation which the plaice has, the goldfish has a twofold cycle in the year. The index reaches its second and higher maximum in August, and falls thereafter till the end of the year. That it should begin to fall so soon, and fall so quickly, merely means that late autumn is a time of growth; the fish are not losing weight, but growing longer†.

* Cf. Kichiro Sasaki, *Tohoku Sci. Reports* (4), I, pp. 239-260, 1926.

† Much has been written on the weight-length index in fishes. See (*int. al.*) A. Meek, The growth of flatfish, *Northumberland Sea Fisheries Ctee*, 1905, p. 58; W. J. Crozier, Correlations of weight, length, etc., in the weakfish, *Cynoscion*

It is the rule in fishes and other cold-blooded vertebrates that growth is asymptotic and size indeterminate, while in the warm-blooded growth comes, sooner or later, to an end. But the characteristic form is established earlier in the former case, and changes less, save for the minor fluctuations we have spoken of. In the higher animals, such as ourselves, the whole course of life is attended by constant alteration and modification of form; and

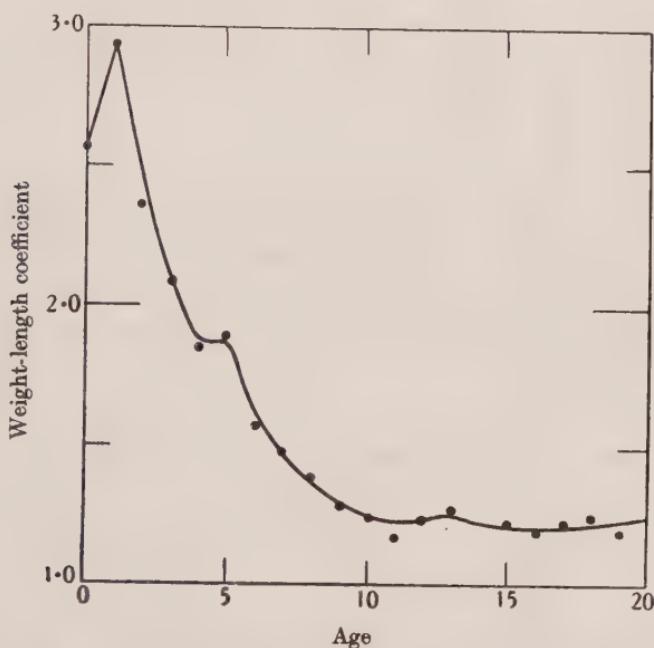


Fig. 52. The ponderal index, or weight-length coefficient, in man. From Quetelet's data.

we may use our weight-length formula, or ponderal index, to illustrate (for instance) the changing relation between height and weight in boyhood, of which we spoke before (Fig. 52).

regalis, Bull. U.S. Bureau of Fisheries, XXXIII, pp. 141-147, 1913; Selig Hecht, Form and growth in fishes, Journ. of Morphology, XXVII, pp. 379-400, 1916; J. Johnstone (Plaice), Trans. Liverpool Biolog. Soc. XXV, pp. 186-224, 1911; J. J. Tesch (Eel), Journ. du Conseil, III, 1927; Frances N. Clark (Sardine), Calif. Fish. Bulletin, No. 19, 1928 (with full bibliography). For a discussion on statistical lines, apart from any assumptions such as the "law of the cubes," see G. Duncker, Korrelation zwischen Länge u. Gewicht, etc., Wissensch. Meeresuntersuch. Helgoland, XV, pp. 1-26, 1923.

*The weight-length coefficient, or ponderal index, k , in young Belgians
(From Quetelet's figures)*

Age (years)	W/L^3	Age (years)	W/L^3
0	2.55	10	1.25
1	2.92	11	1.18
2	2.34	12	1.23
3	2.08	13	1.29
4	1.87	14	1.23
5	1.72	15	1.23
6	1.56	16	1.28
7	1.48	20	1.30
8	1.39	25	1.36
9	1.29		

The infant is plump and chubby, and the ponderal index is at its highest at a year old. As the boy grows, it is in stature that he does so most of all; his ponderal index falls continually, till the growing years are over, and the lad "fills out" and grows stouter again. During prenatal life the index varied little, and less than we might suppose:

*Relation between length and weight of the human foetus
(From Scammon's data)*

Length cm.	Weight gm.	W/L^3
7.7	13	2.9
12.3	41	2.2
17.3	115	2.2
22.3	239	2.2
27.2	405	2.0
32.3	750	2.2
37.2	1163	2.3
42.2	1758	2.3
46.9	2389	2.3
51.7	3205	2.3

As a further illustration of the rate of growth, and of unequal growth in various directions, we have figures for the ox, extending over the first three years of the animal's life, and giving (1) the weight of the animal, month by month, (2) the length of the back, from occiput to tail, and (3) the height to the withers. To these I have added (4) the ratio of length to height, (5) the weight-length coefficient, k , and (6) a similar coefficient, or index-number, k' , for

the height of the animal. All these ratios change as time goes on. The ratio of length to height increases, at first considerably, for the legs seem disproportionately long at birth in the ox, as in other

*Relations between the weight and certain linear dimensions of the ox
(Data from Cornevin*, abbreviated)*

Age months	Weight kgm.	Length of back m.	Height m.	L/H	$k = W/L^3$	$k' = W/H^3$
0	37	0.78	0.70	1.11	0.78	1.08
1	55	0.94	0.77	1.22	0.66	1.21
2	86	1.09	0.85	1.28	0.67	1.41
3	121	1.21	0.94	1.28	0.69	1.46
4	150	1.31	0.95	1.38	0.66	1.75
5	179	1.40	1.04	1.35	0.65	1.60
6	210	1.48	1.09	1.36	0.64	1.64
7	247	1.52	1.12	1.36	0.70	1.75
8	267	1.58	1.15	1.38	0.68	1.79
9	283	1.62	1.16	1.39	0.66	1.80
10	304	1.65	1.19	1.39	0.68	1.79
11	328	1.69	1.22	1.39	0.67	1.79
12	351	1.74	1.24	1.40	0.67	1.85
13	375	1.77	1.25	1.41	0.68	1.90
14	391	1.79	1.26	1.41	0.69	1.94
15	406	1.80	1.27	1.42	0.69	1.98
16	418	1.81	1.28	1.42	0.70	2.09
17	424	1.83	1.29	1.42	0.69	1.97
18	424	1.86	1.30	1.43	0.66	1.94
19	428	1.88	1.31	1.44	0.65	1.92
20	438	1.88	1.31	1.44	0.66	1.94
21	448	1.89	1.32	1.43	0.66	1.94
22	464	1.90	1.33	1.43	0.68	1.96
23	481	1.91	1.35	1.42	0.69	1.98
24	501	1.91	1.35	1.42	0.71	2.03
25	521	1.92	1.36	1.41	0.74	2.08
26	534	1.92	1.36	1.41	0.75	2.12
27	547	1.93	1.36	1.41	0.76	2.16
28	555	1.93	1.36	1.41	0.77	2.19
29	562	1.93	1.36	1.41	0.78	2.22
30	586	1.95	1.38	1.41	0.79	2.22
31	611	1.97	1.40	1.40	0.80	2.21
32	626	1.98	1.42	1.40	0.80	2.19
33	641	2.00	1.44	1.39	0.81	2.16
34	656	2.01	1.45	1.38	0.81	2.13

ungulate animals; but this ratio reaches its maximum and falls off a little during the third year: so indicating that the beast is growing more in height than length, at a time when growth in both

* Ch. Cornevin, Études sur la croissance, *Arch. de Physiol. norm. et pathol.* (5), IV, p. 477, 1892. Cf. also R. Gärtner, Ueber das Wachstum d. Tiere, *Landwirtsch. Jahresser.* LVII, p. 707, 1922.

dimensions is nearly over*. The ratio W/H^3 increases steadily, and at three years old is double what it was at birth. It is the most variable of the three ratios; and it so illustrates the somewhat obvious but not unimportant fact that k varies most for the dimension which varies least, or grows most uniformly; in other words, that the values of k , as determined at successive epochs for any one dimension, are a measure of the variability of the other two.

The same ponderal index serves as an index of "build," or bodily proportion; and its mean values have been determined for various ages and for many races of mankind. Within one and the

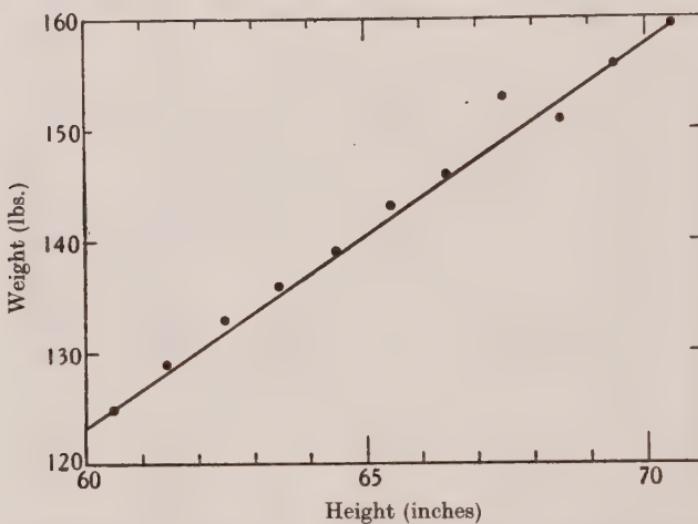


Fig. 53. Ratio of height to weight in man. From Goringe's data.

same race it varies with stature; for tall men, and boys too, are apt to be slender and lean, and short ones to be thickset and strong. And so much does the weight-length ratio change with build or stature that, in the following table of mean heights and weights of men between five and six feet high, it will be seen that weight, instead of varying as the cube of the height, is (within the limits shewn) in nearly simple linear relation to it (Fig. 53)†.

* As a matter of fact, the data shew that the animal grows under 7 per cent. in length, but over 11 per cent. in height, between the twentieth and the thirtieth month of its age.

† Had the weights varied as the cube of the height, the tallest men should have weighed close on 200 lb., instead of 160 lb.

*Ratio of height to weight in man**

No. of instances	Height in.	Weight lb.	W/H	W/H^3
59	60.5	125	2.07	5.62
118	61.5	129	2.13	5.55
220	62.5	133	2.13	5.45
285	63.5	136	2.14	5.30
327	64.5	139	2.15	5.19
386	65.5	143	2.18	5.09
346	66.5	146	2.20	4.97
289	67.5	153	2.27	4.96
220	68.5	151	2.20	4.71
116	69.5	156	2.24	4.64
58	70.5	160	2.27	4.57

The same index may be used as a measure of the condition, even of the quality, of an animal; three Burmese elephants had the following heights, weights, and reputations†:

	Height	Weight	W/H^3	
A	7 ft. 10½ in.	7,511 lb.	1.54	A famous elephant
B	8 1	7,216	1.36	A good elephant
C	7 5	4,756	1.15	A weak, poor elephant

But a great African elephant, 10 ft. 10 in. high, weighed 14,640 lb.‡: whence the weight-height coefficient was no more than 1.15. That is to say, the African elephant is considerably taller than the Indian, and the weight-height ratio is correspondingly less.

Lastly, by means of the same index we may judge, to a first rough approximation, the weight of a large animal such as a whale, where weighing is out of the question. Sigurd Rusting has given us many measurements, and many foetal weights, from the Antarctic whale-fishery: among which, choosing at random, we find that a certain foetus of the blue whale, or Sibbald's rorqual, measured 4 ft. 6 in. long, and weighed 23 kilos, or say 46 lb. A whale of the same kind, 45 ft. long, should then weigh 46×10^3 lb., or about 23 tons; and one of 90 ft., 23×2^3 tons, or over 180 tons. Again in seven young unborn whales, measuring from 39 to 54 inches and weighing from 10 to 23 kilos, the mean value of the index was found

* Data from Sir C. Goringe, *The English Convict*, H.M. Stationery Office, 1913. See also J. A. Harris and others, *The Measurement of Man*, Minnesota, 1930, p. 41.

† Data from A. J. Milroy, *On the management of elephants*, Shillong, 1921.

‡ D. P. Quireng, in *Growth*, III, p. 9, 1939.

to be 15·2, in gramme-inches. From this we calculate the weight of the great rorqual, as follows:

$$\text{At } 25 \text{ ft., or } 300 \text{ inches, } W = \frac{15 \cdot 2 \times 300^3}{100} = 4,100,000 \text{ g.}$$

$$= 4,100 \text{ kg.}$$

$$= 4 \text{ tons, nearly.}$$

At 50 ft., $W = 4 \times 2^3$ tons	= 32 tons.
100 ft. = 32×2^3 tons	= 256 tons.
106 tons (the largest known)	$W = 305$ tons, nearly.

The two independent estimates are in close agreement.

Of surface and volume

While the weight-length relation is of especial importance, and is wellnigh fundamental to the understanding of growth and form and magnitude, the corresponding relation of surface-area to weight or volume has in certain cases an interest of its own. At the surface of an animal heat is lost, evaporation takes place, and oxygen may be taken in, all in due proportion as near as may be to the bulk of the animal; and again the bird's wing is a surface, the area of which *must* be in due proportion to the size of the bird. In hollow organs, such as heart or stomach, area is the important thing rather than weight or mass; and we have seen how the brain, an organ not obviously but essentially and developmentally hollow, tends to shew its due proportions when reckoned as a *surface* in comparison with the creature's *mass*.

Surface cannot keep pace with increasing volume in bodies of similar form; wing-area does not and cannot long keep pace with the bird's increasing bulk and weight, and this is enough of itself to set limits to the size of the flying bird. It is the ratio between square-root-of-surface and cube-root-of-volume which should, in theory, remain constant; but as a matter of fact this ratio varies (up to a certain extent) with the circumstances, and in the case of the bird's wing with varying modes and capabilities of flight. The owl, with his silent, effortless flight, capable of short swift spurts of attack, has the largest spread of wings of all; the kite outstrips the other hawks in spread of wing, in soaring, and perhaps in speed.

Stork and seagull have a great expanse of wing; but other skilled and speedy fliers have long narrow wings rather than large ones. The peregrine has less wing-area than the goshawk or the kestrel; the swift and the swallow have less than the lark.

*Mean ratio, $\sqrt[2]{S}/\sqrt[3]{W}$, between wing-area and weight of birds
(From Mouillard's data)*

		Ratio
Owls	1 species	2.2
Hawks	7 "	1.7
Gulls	1 "	1.7
Waders	3 "	1.7
Petrels	2 "	1.4
Plovers	3 "	1.4
Passerines	4 "	1.3
Ducks	2 "	1.2

To measure the length of an animal is easy, to weigh it is easier still, but to estimate its surface-area is another thing. Hence we know but little of the surface-weight ratios of animals, and what we know is apt to be uncertain and discrepant. Nevertheless, such data as we possess average down to mean values which are more uniform than we might expect*.

Mean ratio, $\sqrt[2]{S}/\sqrt[3]{W}$, in various animals (cm. gm. units)

Ape	11.8	Sheep (shorn)	8
Man	11	Snake	12.5
Dog	10-11	Frog	10.6
Cat, horse	10	Birds	10
Rabbit	9.75	Tortoise	10
Cow, pig, rat	9		

A further note on unequal growth, or heterogony

An organism is so complex a thing, and growth so complex a phenomenon, that for growth to be so uniform and constant in all the parts as to keep the whole shape unchanged would indeed be an unlikely and an unusual circumstance. Rates vary, proportions change, and the whole configuration alters accordingly. In so humble a creature as a medusoid, manubrium and disc grow at different rates, and certain sectors of the disc faster than others, as when the little *Ephyra*-larva "develops" into the great *Aurelia*-jellyfish. Many fishes grow from youth to age with no visible,

* From Fr. G. Benedict, *Oberflächenbestimmung verschiedener Tiergattungen, Ergebnisse d. Physiologie*, xxxvi, pp. 300-346, 1934 (with copious bibliography).

hardly a measurable, change of form*; but the shapes and looks of man and woman go on changing long after the growing age is over, even all their lives long. A centipede has its many pairs of legs alike, to all intents and purposes; they begin alike and grow uniformly. But a lobster has his great claws and his small, his lesser legs, his swimmerets and the broad flaps of his tail; all these begin alike, and diverse rates of growth make up the difference between them. Moreover, we may sometimes watch a single limb growing to an unusual size, perhaps in one sex and not in the other, perhaps on one side and not on the other side of the body: such are the "horns," or mandibles, of the stag-beetle, only conspicuous in the male, and the great unsymmetrical claws of the lobster, or of that extreme case the little fiddler-crab (*Uca pugnax*). For such well-marked cases of differential growth-ratio between one part and another, Julian Huxley has introduced the term *heterogony*†.

Of the fiddler-crabs some four hundred males were weighed, in twenty-five graded samples all nearly of a size, and the weights of the great claw and of the rest of the body recorded separately. To begin with the great claw was about 8 per cent., and at the end about 38 per cent., of the total weight of the un mutilated body. In the female the claw weighs about 8 per cent. of the whole from beginning to end; and this contrast marks the disproportionate, or heterogonic, rate of growth in the male. We know nothing about the actual rate of growth of either body or claw, we cannot plot either against time; but we know the relative proportions, or relative rates of growth of the two parts of the animal, and this is all that matters meanwhile. In Fig. 54, we have set off the successive weights of the body as abscissae, up to 700 mgm., or about one-third of its weight in the adult animal; and the ordinates represent the corresponding weights of the claw. We see that the ratio between the two magnitudes follows a curve, apparently an exponential curve; it does in fact (as Huxley has shewn) follow a compound

* Cf. S. Hecht, Form and growth in fishes, *Journ. Morphology*, xxvii, pp. 379-400, 1916; F. S. and D. W. Hammett, Proportional length-growth of garfish (*Lepidosteus*), *Growth*, iii, pp. 197-209, 1939.

† See *Problems of Relative Growth*, 1932, and many papers quoted therein. The term, as Huxley tells us, had been used by Pézard; but it had been used, in another sense, by Rolleston long before to mean an alternation of generations, or production of offspring dissimilar to the parent.

interest law, which (calling y and x the weights of the claw and of the rest of the body) may be expressed by the usual formula for compound interest,

$$y = bx^k, \text{ or } \log y = \log b + k \log x;$$

and the coefficients (b and k) work out in the case of the fiddler-crab, to begin with, at

$$y = 0.0073 x^{1.62}$$

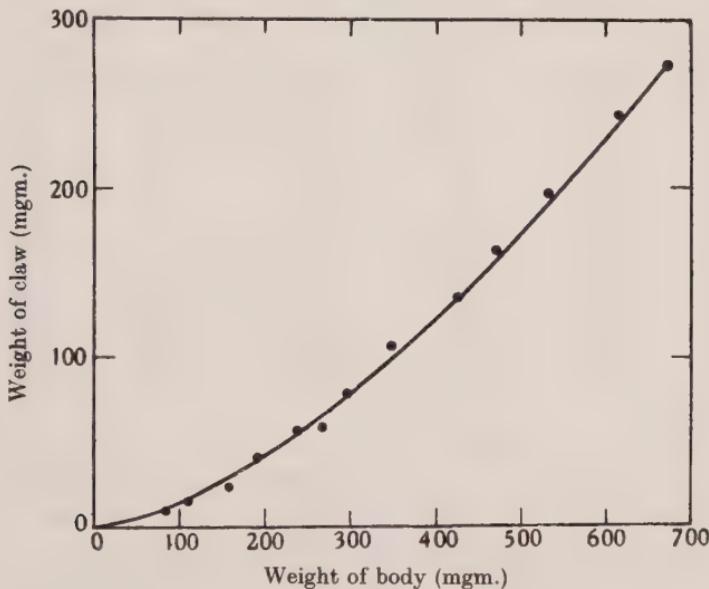


Fig. 54. Relative weights of body and claw in the fiddler-crab (*Uca pugnax*).

But after a certain age, or certain size, these coefficients no longer hold, and new coefficients have to be found. Whether or no, the formula is mathematical rather than biological; there is a lack of either biological or physical significance in a growth-rate which happens to stand, during part of an animal's life, at 62 per cent. compound interest.

Julian Huxley holds, and many hold with him, that the exponential or logarithmic formula, or the compound-interest law, is of general application to cases of differential growth-rates. I do not find it to be so: any more than we have found organ, organism or population to increase by compound interest or geometrical progression, save

under exceptional circumstances and in transient phase. Undoubtedly many of Huxley's instances shew increase by compound interest, during a phase of rapid and unstinted growth; but I find many others following a simple-interest rather than a compound-interest law.

*Relative weights of claw and body in fiddler-crabs (*Uca pugnax*).*

(Data abbreviated from Huxley, Problems of Relative Growth, p. 12)

Wt. of body less claw (mgm.)	Wt. of claw	Ratio %	Wt. of body	Wt. of claw	Ratio %
58	5	8·6	618	243	39·3
80	9	11·2	743	319	42·9
109	14	12·8	872	418	47·9
156	25	16·0	983	461	46·9
200	38	19·0	1080	537	49·7
238	53	22·3	1166	594	50·9
270	59	21·9	1212	617	50·9
300	78	26·0	1299	670	51·6
355	105	29·7	1363	699	51·3
420	135	32·1	1449	773	53·7
470	165	35·1	1808	1009	55·8
536	196	36·6	2233	1380	61·7

In the common stag-beetle (*Lucanus cervus*) we have the following measurements of mandible and elytron or wing-case: which two organs make up the bulk of, and may for our purpose be held as constituting, the "total length" of the beetle. Here a simple equation meets the case; in other words, the length of elytron or of mandible plotted against total length gives what is to all intents and purposes a straight line, indicating a simple-interest rather than a compound-interest rate of increase.

*Measurements of 48 stag-beetles (*Lucanus cervus*)* (mm.)*

Number of specimens	1	4	5	10	5	7	11	5
Length, total (x)	31·0	38·7	40·5	42·6	45·0	46·9	49·2	53·6
Length of elytron (y)	25·0	30·9	31·5	32·6	33·8	35·1	36·4	39·2
(,, calculated) (y')	26·9	30·8	31·7	32·8	34·0	35·0	36·2	38·5
Length of mandible (z)	6·0	7·8	9·0	10·0	11·2	11·9	12·8	14·4
(,, calculated) (z')	5·9	7·7	9·3	10·1	11·0	11·7	12·6	14·2

* Data, from Julian Huxley, after W. Bateson and H. H. Brindley, in *P.Z.S.* 1892, pp. 585-594.

From the observed data we may solve, by the method of least squares, the simple equations

$$y = a + bx, \quad z = c + dx,$$

or in other words, find the equations of the straight lines in closest agreement with the observed data. The solutions are as follows*:

$$y = 11.02 + 0.512x, \text{ and } z = -5.64 + 0.368x,$$

the two coefficients 0.368 and 0.512 signifying the difference between the rates of increase of the two organs. The number of samples is not very large, and some deviation is to be expected; nevertheless, the calculated straight lines come close to the observed values.

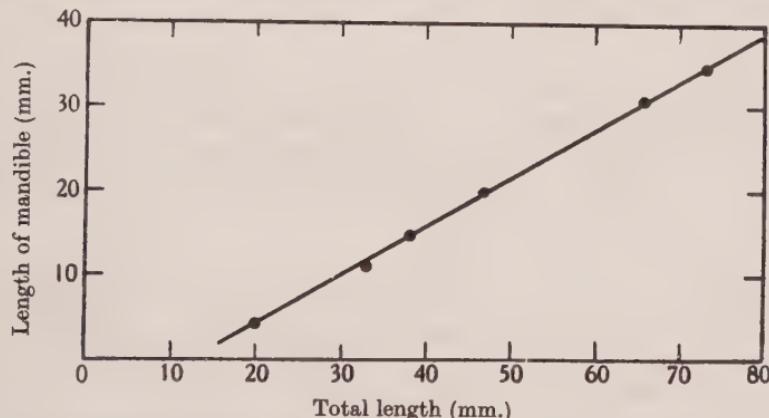


Fig. 55. Relative growth of body and mandible in reindeer-beetle (*Cyclommatus tarandus*).

The reindeer-beetle (*Cyclommatus tarandus*), belonging to the same family, shews much the same thing. The mandible grows in approximately linear ratio to the body, save that it tends to be at first a little above, and later on a little below, this linear ratio (Fig. 55).

Measurements of Cyclommatus tarandus† (mm.)

Length of mandible (y)	3.9	10.7	14.1	19.9	24.0	30.7	34.5
Total length (x)	20.4	33.1	38.4	47.3	54.2	66.1	74.0
Total length calculated:	20.3	31.9	37.7	47.5	54.5	65.9	72.4
$x = 1.7y + 13.7$							

* As determined for me by Dr A. C. Aitken, F.R.S.

† Data, much abbreviated, from Huxley, after E. Dudich, *Archiv f. Naturgesch.* (A), 1923.

The facial and cranial parts of a dog's skull tend to grow at different rates (Fig. 56); and changes in the ratio between the two go a long way to explain the differences in shape between one dog's skull and another's, between the greyhound's and the pug's. But using Huxley's own data (after Becher) for the sheepdog, I find the ratio between the facial and cranial portions of the skull to be, once again, a simple linear one.

Measurements of skull of sheep-dog (30 specimens) (mm.)*

Mean length of facial region (y)	22·0	48·3	58·0	73·5	89·1	102·0	112·0
Mean length of cranial region (x)	42·0	65·3	74·5	85·5	99·3	112·6	120·0
Calculated values for cranial region: $x = 22·7 + 0·88y$	42·1	65·2	73·7	87·4	97·1	112·5	121·2

And now, returning to the fiddler-crab, we find that after the crab has reached a certain size and the first phase of rapid growth is over, claw and body grow in simple linear relation to one another, and the heterogonic or compound-interest formula is no longer required:

Fiddler-crab (Uca pugnax): ratio of growth-rates, in later stages, of claw and body (mgm.)

Weight of body less claw (x)	872	983	1080	1165	1212	1291	1363	1449
Weight of large claw (y)	418	461	537	594	617	670	699	778
Do., calculated: $y = 0·6x - 110$	413	480	538	590	617	665	708	759

* Data from A. Becher, in *Archiv f. Naturgesch.* (A), 1923; see Huxley, *Problems of Relative Growth*, p. 18, and *Biol. Centralbl. loc. cit.* Here, and in the previous case of *Cyclommatus*, the equation has been arrived at in a very simple way. Take any two values, x_1 , x_2 , and the corresponding values, y_1 , y_2 . Then let

$$\frac{x - x_1}{x_2 - x_1} = \frac{y - y_1}{y_2 - y_1},$$

$$\text{e.g. } \frac{x - 65·3}{112·6 - 65·3} = \frac{y - 48·3}{102·0 - 48·3},$$

$$\text{or } \frac{x - 65·3}{47·3} = \frac{y - 48·3}{53·7},$$

from which $x = 22·7 + 0·88y$.

We may with advantage repeat this process with other values of x and y ; and take the mean of the results so obtained.

Once again we find close agreement between the observed and calculated values, although the observations are somewhat few and the equation is arrived at in a simple way. We may take it as proven that the relation between the two growth-rates is essentially linear.

A compound-interest law of growth occurs, as Malthus knew, in cases, and at times, of rapid and unrestricted growth. But unrestricted growth occurs under special conditions and for brief

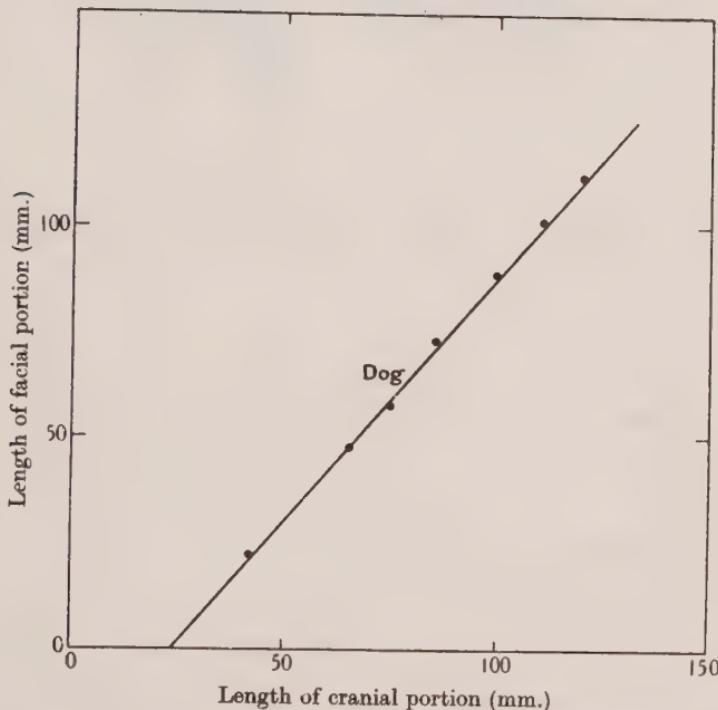


Fig. 56. Relative growth of the cranial and facial portions of the skull in the sheepdog. Cf. Huxley, p. 18, after Becher.

periods; it is the exception rather than the rule, whether in a population or in the single organism. In cases of differential growth the compound-interest law manifests itself, for the same reason, when one of the two growth-rates is rapid and "unrestricted," and when the discrepancy between the two growth-rates is consequently large, for instance in the fiddler-crabs. The compound-interest law is a very natural mode of growth, but its range is

limited. A linear relation, or simple-interest law, seems less likely to occur; but the fact is, it does occur, and occurs commonly.

On so-called dimorphism

In a well-known paper, Bateson and Brindley shewed that among a large number of earwigs collected in a particular locality, the males fell into two groups, characterised by large or by small

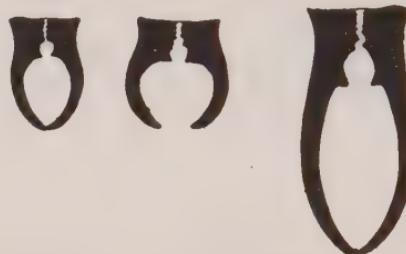


Fig. 57. Tail-forceps of earwig. From Martin Burr, after Willi Kuhl.

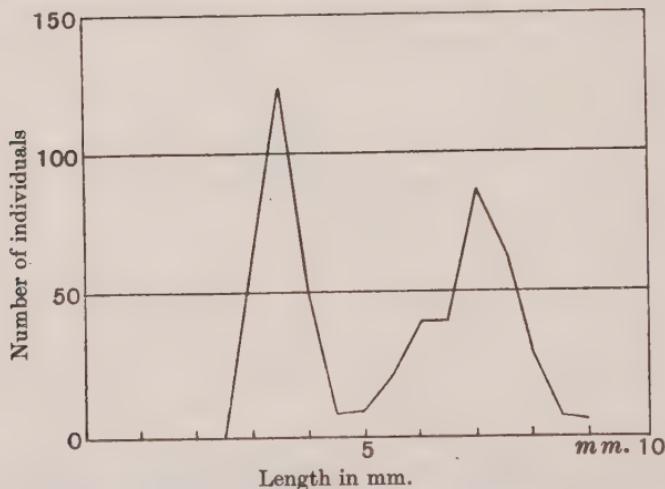


Fig. 58. Variability of length of tail-forceps in a sample of earwigs.
After Bateson and Brindley, P.Z.S. 1892, p. 588.

tail-forceps (Fig. 57), with few instances of intermediate magnitude*. This distribution into two groups, according to magnitude, is illustrated in the accompanying diagram (Fig. 58); and the

* W. Bateson and H. H. Brindley, On some cases of variation in secondary sexual characters [*Forficula*, *Xylotrupa*], statistically examined, P.Z.S. 1892, pp. 585–594. Cf. D. M. Diakonow, On dimorphic variability of *Forficula*, Journ. Genet. xv, pp. 201–232, 1925; and Julian Huxley, The bimodal cephalic horn of *Xylotrupa*, ibid. xviii, pp. 45–53, 1927.

phenomenon was described, and has been often quoted, as one of dimorphism or discontinuous variation. In this diagram the time-element does not appear; but it looks as though it lay close behind. For the two *size-groups* into which the tails of the earwigs fall look curiously like two *age-groups* such as we have already studied in a fish, where the *ages* and therefore also the *magnitudes* of a random sample form a discontinuous series (Fig. 59). And if, instead of measuring the whole length of our fish, we had confined ourselves to particular parts, such as head, or tail or fin, we should have obtained discontinuous curves of distribution for the magnitudes

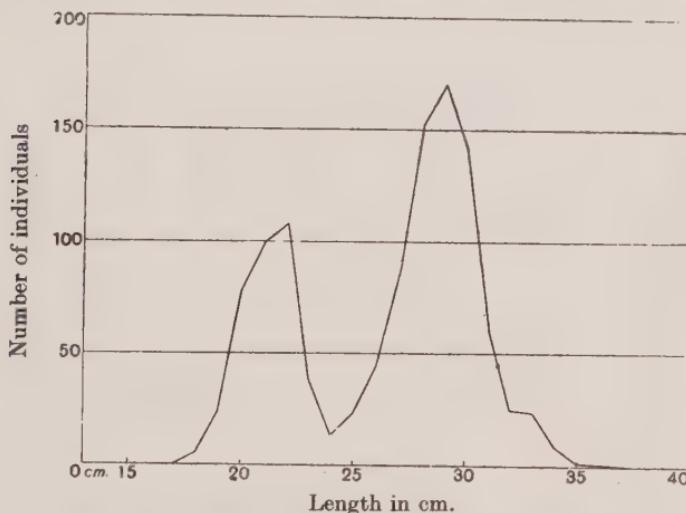


Fig. 59. Length of body in a random sample of plaice.

of these organs, just as for the whole body of the fish, and just as for the tails of Bateson's earwigs. The differences, in short, with which Bateson was dealing were a question of magnitude, and it was only natural to refer these diverse magnitudes to diversities of growth; that is to say, it seemed natural to suppose that in this case of "dimorphism," the tails of the one group of earwigs (which Bateson called the "high males") had either grown faster, or had been growing for a longer period of time, than those of the "low males." If the whole random sample of earwigs were of one and the same age, the dimorphism would appear to be due to two alternative values for the mean growth-rate, individual earwigs varying around one mean or the other. If, on the other hand, the

two groups of earwigs were of different ages, or had passed through one moult more or less, the phenomenon would be simple indeed, and there would be no more to be said about it*. Diakonow made the not unimportant observation that in earwigs living in unfavourable conditions only the short-tailed type tended to appear.

In apparent close analogy with the case of the earwigs, and in apparent corroboration of their dimorphism being due to age, Fritz Werner measured large numbers of water-fleas, all apparently adult, found his measurements falling into groups and so giving multimodal curves. The several cusps, or modes, he interpreted without difficulty as indicating differences of age, or the number of moults which the creatures had passed through† (Fig. 60).

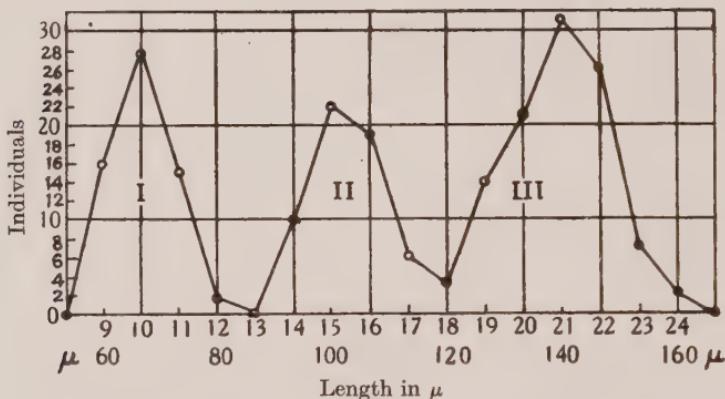


Fig. 60. Measurements of the dorsal edge in a population of *Chydorus sphaericus*, a water-flea. From Fritz Werner.

An apparently analogous but more difficult case is that of a certain little beetle, *Onthophagus taurus*, which bears two "horns" on its head, of variable size or prominence. Linnaeus saw in it a single species, Fabricius saw two; and the question long remained an open one among the entomologists. We now know that there are two "modes," two predominant sizes in a continuous range of

* The number of moults is known to be variable in many species of Orthoptera, and even occasionally in higher insects; and how the number of moults may be influenced by hunger, damp or cold is discussed by P. P. Calvert, *Proc. Amer. Philos. Soc.* LXVIII, p. 246, 1929. On the number of moults in earwigs, see E. B. Worthington, *Entomologist*, 1926, and W. K. Weyrauch, *Biol. Centralbl.* 1929, pp. 543-558.

† Fritz Werner, Variationsanalytische Untersuchungen an Chydoren, *Ztschr. f. Morphologie u. Oekologie d. Tiere*, II, pp. 58-188, 1924.

variation*. In the "complete metamorphosis" of a beetle there is no room for a moult more or less, and the reason for the two modal sizes remains hidden (Fig. 61).

But new light has been thrown on the case of the earwigs, which may help to explain other obscure diversities of shape and size within the class of insects. At metamorphosis, and even in a simple moult, the external organs of an insect may often be seen to unfold, as do, for instance, the wings of a butterfly; they then quickly harden, in a form and of a size with which ordinary gradual growth

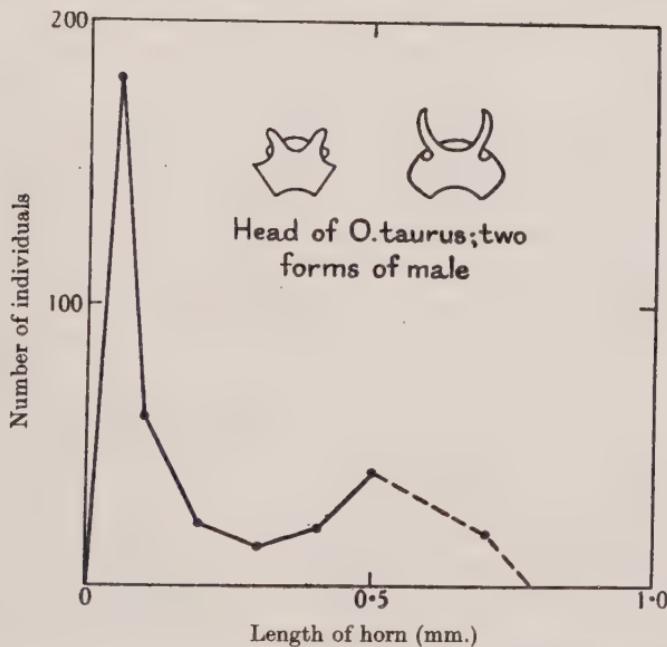


Fig. 61. Two forms of the male, in the beetle *Onthophagus taurus*.

has had nothing directly to do. This is a very peculiar phenomenon, and marks a singular departure from the usual interdependence of growth and form. When the nymph, or larval earwig, is about to shed its skin for the last time, the tail-forceps, still soft and tender, are folded together and wrapped in a sheath; they need to be *distended*, or inflated, by a combined pressure of the body-fluid (or haemolymph) and an intake of respiratory air. If all goes well,

* René Paulian, *Bull. Soc. Zool. Fr.* 1933; also *Le polymorphisme des mâles de Coléoptères*, Paris, 1935, p. 8.

the forceps expand to their full size; if the creature be weak or underfed, inflation is incomplete and the tail-forceps remain small. In either case it is an affair of a few critical moments during the final ecdysis; in ten minutes or less, the chitin has hardened, and shape and size change no more. Willi Kuhl, who has given us this interesting explanation, suggests that the dimorphism observed by Bateson and by Diakonow is not an essential part of the phenomenon; he has found it in one instance, but in other and much larger samples he has found all gradations, but only a single, well-marked unimodal peak*.

The effect of temperature†

The rates of growth which we have hitherto dealt with are mostly based on special investigations, conducted under particular local conditions; for instance, Quetelet's data, so far as we have used them to illustrate the rate of growth in man, are drawn from his study of the Belgian people. But apart from that "fortuitous" individual variation which we have already considered, it is obvious that the normal rate of growth will be found to vary, in man and in other animals, just as the average stature varies, in different localities and in different "races." This phenomenon is a very complex one, and is doubtless a resultant of many undefined contributory causes; but we at least gain something in regard to it when we discover that rate of growth is directly affected by temperature, and doubtless by other physical conditions. Réaumur was the first to shew, and the observation was repeated by Bonnet‡, that the rate of growth or development of the chick was dependent on temperature, being retarded at temperatures below and somewhat

* Willi Kuhl, Die Variabilität der abdominalen Körperanhänge bei *Forficula*, *Ztsch. Morph. u. Oek. d. Tiere*, XII, p. 299, 1924. Cf. Malcolm Burr, *Discovery*, 1939, pp. 340–345.

† The temperature limitations of life, and to some extent of growth, are summarised for a large number of species by Davenport, *Exper. Morphology*, cc. viii, xviii, and by Hans Przibram, *Exp. Zoologie*, IV, c. v.

‡ Réaumur, *L'art de faire éclore et élever en toute saison des oiseaux domestiques, soit par le moyen de la chaleur du fumée, soit par le moyen de celle du feu ordinaire*, Paris, 1749. He had also studied, a few years before, the effects of heat and cold on growth-rate and duration of life in caterpillars and chrysalids: *Mémoires*, II, p. 1, *de la durée de la vie des crisalides* (1736). See also his *Observations du Thermomètre*, etc., *Mém. Acad.*, Paris, 1735, pp. 345–376.

accelerated at temperatures above the normal temperature of incubation, that is to say the temperature of the sitting hen. In the case of plants the fact that growth is greatly affected by temperature is a matter of familiar knowledge; the subject was first carefully studied by Alphonse De Candolle, and his results and those of his followers are discussed in the textbooks of botany*.

That temperature is only one of the climatic factors determining growth and yield is well known to agriculturists; and a method of "multiple correlation" has been used to analyse the several influences of temperature and of rainfall at different seasons on the future yield of our own crops†. The same joint influence can be recognised in the bamboo; for it is said (by Lock) that the growth-rate of the bamboo in Ceylon is proportional to the humidity of the atmosphere, and again (by Shibata) that it is proportional to the temperature in Japan. But Blackman‡ suggests that in Ceylon temperature conditions are all that can be desired, but moisture is apt to be deficient, while in Japan there is rain in abundance but the average temperature is somewhat low: so that in the one country it is the one factor, and in the other country the other, whose variation is both conspicuous and significant. After all, it is probably rate of evaporation, the joint result of temperature and humidity, which is the crux of the matter§. "Climate" is a subtle thing, and includes a sort of micro-meteorology. A sheltered corner has a climate of its own; one side of the garden-wall has a different climate to the other; and deep in the undergrowth of a wood celandine and anemone enjoy a climate many degrees warmer than what is registered on the screen||.

Among the mould-fungi each several species has its own optimum temperature for germination and growth. At this optimum temperature growth is further accelerated by increase of humidity; and the further we depart from the optimum temperature, the narrower becomes the range of humidity within which growth can proceed¶. Entomologists know, in like manner, how over-abundance of an insect-pest comes, or is apt to come, with a double optimum of temperature and humidity.

* Cf. (*int. al.*) H. de Vries, Matériaux pour la connaissance de l'influence de la température sur les plantes, *Arch. Néerlandaises*, v, pp. 385–401, 1870; C. Linsser, Periodische Erscheinungen des Pflanzenlebens, *Mém. Acad. des Sc., St Pétersbourg* (7), xi, XII, 1867–69; Köppen, Wärme und Pflanzenwachstum, *Bull. Soc. Imp. Nat., Moscou*, XLIII, pp. 41–110, 1871; H. Hoffmann, Thermische Vegetations-constanten, *Ztschr. Oesterr. Ges. f. Meteorologie*, XVII, pp. 121–131, 1881; Phenologische Studien, *Meteorolog. Ztschr.* III, pp. 113–120, 1886.

† See (*int. al.*) R. H. Hooker, *Journ. Roy. Statist. Soc.* 1907, p. 70; *Journ. Roy. Meteor. Soc.* 1922, p. 46.

‡ F. F. Blackman, *Ann. Bot.* xix, p. 281, 1905.

§ Száva-Kovátz, in *Petermann's Mitteilungen*, 1927, p. 7.

|| Cf. E. J. Salisbury, On the oecological aspects of Meteorology, *Q.J.R. Meteorol. Soc.* July 1939.

¶ R. G. Tomkins, *Proc. R.S. (B)*, cv, pp. 375–401, 1929.

The annexed diagram (Fig. 62), showing growth in length of the roots of some common plants at various temperatures, is a sufficient illustration of the phenomenon. We see that there is always a certain temperature at which the rate is a maximum; while on either side of the optimum the rate falls off, after the fashion of the normal curve of error. We see further, from the data given by Sachs and others, that the optimum is very much the same for all the common plants of our own climate. For these it is somewhere about 26° C.

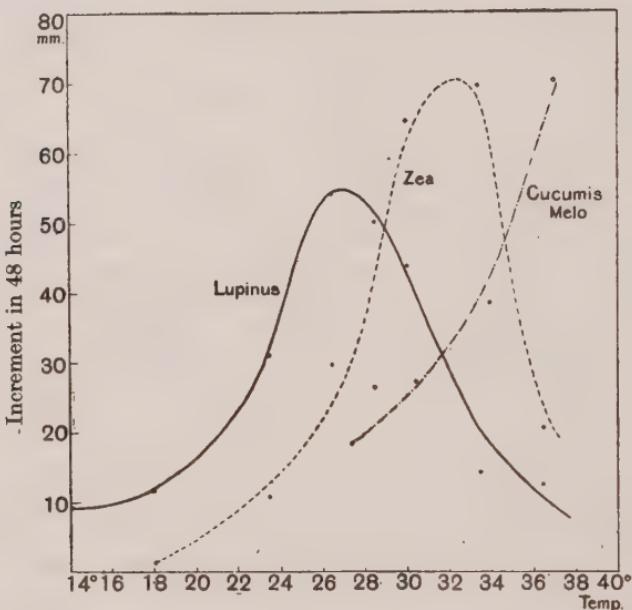


Fig. 62. Relation of rate of growth to temperature in certain plants. From Sachs's data.

(say 77° F.), or about the temperature of a warm summer's day; while it is considerably higher, naturally, in such plants as the melon or the maize, which are at home in warmer countries than our own. The bacteria have, in like manner, their various optima, and sometimes a high one. The tuberculosis-bacillus, as Koch shewed, only begins to grow at about 28° C., and multiplies most rapidly at 37–38°, the body-temperature of its host.

The setting and ripening of fruit is a phase of growth still more dependent on temperature; hence it is a "delicate test of climate," and a proof of its constancy, that the date-palm grows but bears

no fruit in Judaea, and the vine bears freely at Eshcol, but not in the hotter country to the south*. Shellfish have their own appropriate spawning-temperatures; it needs a warm summer for the oyster to shed her spat, and *Hippopus* and *Tridacna*, the great clams of the coral-reefs, only do so when the water has reached the high temperature of 30° C. For brown trout, 6° C. is found to be a critical temperature, a minimum short of which they do not grow at all; it follows that in a Highland burn their growth is at a standstill for fully half the year†.

That a rise of temperature accelerates growth is but part of the story, and is not always true. Several insects, experimentally reared, have been found to diminish in size as the temperature increased‡; and certain flies have been found to be larger in their winter than their summer broods. The common copepod, *Calanus finmarchicus*, has spring, summer and autumn broods, which (at Plymouth§) are large, middle-sized and small; but the large spring brood are hatched and reared in the cold "winter" water, and the small autumn-winter brood in the warmest water of the year. In the cold waters of Barents Sea *Calanus* grows larger still; of an allied genus, a large species lives in the Antarctic, a small one in the tropics, a middle-sized is common in the temperate oceans. The large size of many Arctic animals, coelenterates and crustaceans, is well known; and so is that of many tropical forms, like *Fungia* among the corals, or the great Tritons and Tridacnas among molluscs. Another common phenomenon is the increasing number of males in late summer and autumn, as in the Rotifers and in the above-mentioned Calani. All these things seem somehow related to temperature; but other physical conditions enter into the case, for instance the amount of dissolved oxygen in the cold waters, and the physical chemistry of carbonate of lime in the warm||.

The vast profusion of life, both great and small, in Arctic seas, the multitude of individuals and the unusual size to which many species grow, has been often ascribed to a superabundance of dissolved oxygen, but oxygen alone would not go far. The nutrient salts, nitrates and phosphates, are the

* Cf. J. W. Gregory, in *Geogr. Journ.* 1914, and *Journ. R. Geogr. Soc.* Oct. 1930.

† Cf. C. A. Wingfield, *op. cit. supra*, p. 176.

‡ B. P. Uvarow, *Trans. Ent. Soc. Lond.* LXXIX, p. 38, 1931.

§ W. H. Golightly and Ll. Lloyd, in *Nature*, July 22, 1939.

|| Cf. B. G. Bogorow and others, in the *Journ. M.B.A.* xix, 1933-34.

limiting factor in the growth of that micro-vegetation with which the whole cycle of life begins. The tropical oceans are often very bare of these salts; in our own latitudes there is none too much, and the spring-growth tends to use up the supply. But we have learned from the Discovery Expedition that these salts are so abundant in the Antarctic that plant-growth is never checked for stint of them. Along the Chilean coast and in S.W. Africa, cold Antarctic water wells up from below the warm equatorial current. It is ill-suited for the growth of corals, which build their reefs in the warmer waters of the eastern side; but it teems with nourishment, breeds a plankton-fauna of the richest kind, which feeds fishes preyed on by innumerable birds, the guano of which is sent all over the world. Now and then persistent winds thrust the cold current aside; a new warm current, *el Nino* of the Chileans, upsets the old equilibrium; the fishes die, the water stinks, the birds starve. The same thing happens also at Walfisch Bay, where on such rare occasions dead fish lie piled up high along the shore.

It is curiously characteristic of certain physiological reactions, growth among them, to be affected not merely by the temperature of the moment, but also by that to which the organism has been previously and temporarily exposed. In other words, acclimatisation to a certain temperature may continue for some time afterwards to affect all the temperature relations of the body*. That temporary cold may, under certain circumstances, cause a subsequent acceleration of growth is made use of in the remarkable process known as *vernalisation*. An ingenious man, observing that a winter wheat failed to flower when sown in spring, argued that exposure to the cold of winter was necessary for its subsequent rapid growth; and this he verified by "chilling" his seedlings for a month to near freezing-point, after which they grew quickly, and flowered at the same time as the spring wheat. The economic advantages are great of so shortening the growing period of a crop as to protect it from autumn frosts in a cold climate or summer drought in a hot one; much has been done, especially by Lysenko in Russia, with this end in view†.

The most diverse physiological processes may be affected by temperature. A great astronomer at Mount Wilson, in California, used some idle hours to watch the "trail-running" ants, which run all night and all day. Their speed increases so regularly with the temperature that the time taken to run 30 cm. suffices to tell the

* Cf. Kenneth Mellanby, On temperature coefficients and acclimatisation, *Nature*, 3 August 1940.

† Cf. (*int. al.*) V. H. Blackman, in *Nature*, June 13, 1936.

temperature to 1° C.! Of two allied species, one ran nearly half as fast again as the other, at the same temperature*.

While at low temperatures growth is arrested and at temperatures unduly high life itself becomes impossible, we have now seen that within the range of more or less congenial temperatures growth proceeds the faster the higher the temperature. The same is true of the ordinary reactions of chemistry, and here Van't Hoff and Arrhenius† have shewn that a definite increase in the velocity of the reaction follows a definite increase of temperature, according to an exponential law: such that, for an interval of n degrees the velocity varies as x^n , x being called the "temperature coefficient" for the reaction in question‡. The law holds good throughout a considerable range, but is departed from when we pass beyond certain normal limits; moreover, the value of the coefficient is found to keep to a certain order of magnitude—somewhere about 2 for a temperature-interval of 10° C.—which means to say that the velocity of the reaction is just about doubled, more or less, for a rise of 10° C.

This law, which has become a fundamental principle of chemical mechanics, is applicable (with certain qualifications) to the phenomena of vital chemistry, as Van't Hoff himself was the first to declare; and it follows that, on much the same lines, one may speak of a "temperature coefficient" of growth. At the same time we must remember that there is a very important difference (though we need not call it a fundamental one) between the purely physical and the

* Harlow Shapley, On the thermokinetics of Dolichoderine ants, *Proc. Nat. Acad. Sci.* x, pp. 436–439, 1924.

† Van't Hoff and Cohen, *Studien zur chemischen Dynamik*, 1896; Sv. Arrhenius, *Ztschr. f. phys. Chemie*, iv, p. 226.

‡ For various instances of a temperature coefficient in physiological processes, see (e.g.) Cohen, *Physical Chemistry for... Biologists* (English edition), 1903; Kanitz and Herzog in *Zeitschr. f. Elektrochemie*, xi, 1905; F. F. Blackman, *Ann. Bot.* xix, p. 281, 1905; K. Peter, *Arch. f. Entw. Mech.* xx, p. 130, 1905; Arrhenius, *Ergebn. d. Physiol.* vii, p. 480, 1908, and *Quantitative Laws in Biological Chemistry*, 1915; Krogh in *Zeitschr. f. allgem. Physiologie*, xvi, pp. 163, 178, 1914; James Gray, *Proc. R.S. (B)*, xciv, pp. 6–15, 1923; W. J. Crozier, many papers in *Journ. Gen. Physiol.* 1924; J. Belehradek, in *Biol. Reviews*, v, pp. 1–29, 1930. On the general subject, see E. Janisch, Temperaturabhängigkeit biologischer Vorgänge und ihrer kurvenmässige Analyse, *Pflüger's Archiv*, ccix, p. 414, 1925; G. and P. Hertwig, Regulation von Wachstum... durch Umweltfaktoren, in *Hdb. d. normal. u. pathol. Physiologie*, xvi, 1930.

physiological phenomenon, in that in the former we study (or seek and profess to study) one thing at a time, while in the living body we have constantly to do with factors which interact and interfere; increase in the one case (or change of any kind) tends to be continuous, in the other case it tends to be brought, or to bring itself, to arrest. This is the simple meaning of that *Law of Optimum*, laid down by Errera and by Sachs as a general principle of physiology; namely that *every* physiological process which varies (like growth itself) with the amount or intensity of some external influence, does so under such conditions that progressive increase is followed by progressive decrease; in other words, the function has its *optimum* condition, and its curve shews a definite *maximum*. In the case of temperature, as Jost puts it, it has on the one hand its accelerating effect, which tends to follow Van't Hoff's law. But it has also another and a cumulative effect upon the organism: "Sie schädigt oder sie ermüdet ihn, und je höher sie steigt desto rascher macht sie die Schädigung geltend und desto schneller schreitet sie voran*." It is this double effect of temperature on the organism which gives, or helps to give us our "optimum" curves, which (like all other curves of frequency or error) are the expression, not of a single solitary phenomenon, but of a more or less complex resultant. Moreover, as Blackman and others have pointed out, our "optimum" temperature is ill-defined until we take account also of the *duration* of our experiment; for a high temperature may lead to a short but exhausting spell of rapid growth, while the slower rate manifested at a lower temperature may be the best in the end. The mile and the hundred yards are won by different runners; and maximum rate of working, and maximum amount of work done, are two very different things†.

In the case of maize, a certain series of experiments shewed that the growth in length of the roots varied with the temperature as follows‡:

* On such limiting factors, or counter-reactions, see Putter, *Ztschr. f. allgem. Physiologie*, xvi, pp. 574–627, 1914.

† Cf. L. Errera, *L'Optimum*, 1896 (*Recueil d'œuvres, Physiologie générale*, pp. 338–368, 1910); Sachs, *Physiologie d. Pflanzen*, 1882, p. 233; Pfeffer, *Pflanzenphysiologie*, II, p. 78, 194; and cf. Jost, *Ueber die Reactionsgeschwindigkeit im Organismus, Biol. Centralbl.* xxvi, pp. 225–244, 1906.

‡ After Köppen, *Bull. Soc. Nat. Moscou*, xlIII, pp. 41–101, 1871.

Temperature °C.	Growth in 48 hours mm.
18·0	1·1
23·5	10·8
26·6	29·6
28·5	26·5
30·2	64·6
33·5	69·5
36·5	20·7

Let us write our formula in the form

$$\frac{V_{(t+n)}}{V_t} = x^n, \quad \text{or} \quad \log V_{(t+n)} - \log V_t = n \cdot \log x.$$

Then choosing two values out of the above experimental series (say the second and the second-last), we have $t = 23\cdot5$, $n = 10$, and $V, V' = 10\cdot8$ and $69\cdot5$ respectively.

Accordingly, $\frac{\log 69\cdot5 - \log 10\cdot8}{10} = \log x,$

or $\frac{0\cdot8414 - 0\cdot034}{10} = 0\cdot0808,$

and therefore the temperature-coefficient

$$= \text{antilog } 0\cdot0808 = 1\cdot204 \text{ (for an interval of } 1^\circ \text{ C.)}.$$

This first approximation might be much improved by taking account of all the experimental values, two only of which we have yet made use of; but even as it is, we see by Fig. 63 that it is in very fair accordance with the actual results of observation, within those particular *limits of temperature* to which the experiment is confined.

For an experiment on *Lupinus albus*, quoted by Asa Gray* I have worked out the corresponding coefficient, but a little more carefully. Its value I find to be 1·16, or very nearly identical with that we have just found for the maize; and the correspondence between the calculated curve and the actual observations is now a close one.

Miss I. Leitch has made careful observations of the rate of growth of rootlets of the Pea; and I have attempted a further analysis of her principal results†.

* Asa Gray, *Botany*, p. 387.

† I. Leitch, Some experiments on the influence of temperature on the rate of growth in *Pisum sativum*, *Ann. Bot.* xxx, pp. 25–46, 1916, especially Table III, p. 45. Cf. Priestley and Pearsall, Growth studies, *Ann. Bot.* xxxvi, pp. 224–249, 1922.

In Fig. 64 are shewn the mean rates of growth (based on about a hundred experiments) at some thirty-four different temperatures between $0\cdot8^{\circ}$ and $29\cdot3^{\circ}$, each experiment lasting rather less than twenty-four hours. Working out the mean temperature coefficient for a great many combinations of these values, I obtain a value of $1\cdot092$ per $C.^{\circ}$, or $2\cdot41$ for an interval of 10° , and a mean value for the whole series shewing a rate of growth of just about 1 mm. per hour at a temperature of 20° . My curve in Fig. 64 is drawn from these determinations; and it will be seen that, while it is by no means exact at the lower temperatures, and will fail us altogether at very high temperatures, yet it serves as a satisfactory guide to the relations between rate and temperature within the ordinary limits of healthy growth. Miss Leitch

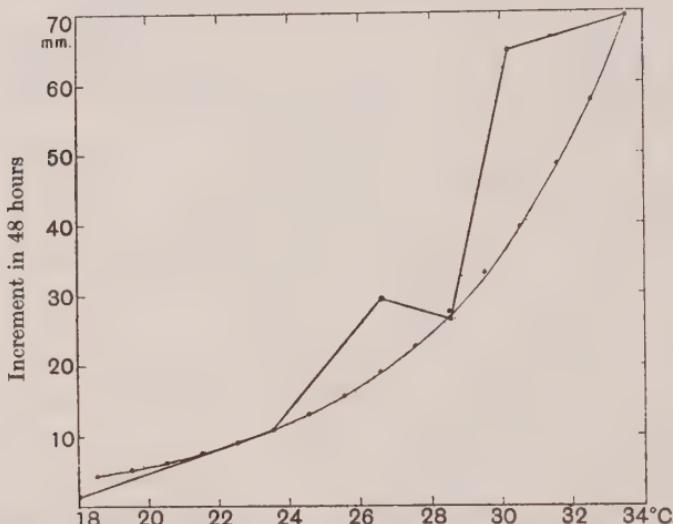


Fig. 63. Relation of rate of growth to temperature in maize. Observed values (after Köppen), and calculated curve.

holds that the curve is *not* a Van't Hoff curve; and this, in strict accuracy, we need not dispute. But the phenomenon seems to me to be one into which the Van't Hoff ratio enters largely, though doubtless combined with other factors which we cannot determine or eliminate.

While the above results conform fairly well to the law of the temperature-coefficient, it is evident that the imbibition of water plays so large a part in the process of elongation of the root or stem that the phenomenon is as much or more a physical than a chemical one: and on this account, as Blackman has remarked, the data commonly given for the rate of growth in plants are apt to be irregular, and sometimes misleading*. We have abundant

* F. F. Blackman, Presidential Address in Botany, *Brit. Assoc.* Dublin, 1908.

illustrations, however, among animals, in which we may study the temperature-coefficient under circumstances where, though the phenomenon is always complicated, true metabolic growth or chemical combination plays a larger rôle. Thus Mlle. Maltaux and Professor Massart* have studied the rate of division in a certain flagellate, *Chilomonas paramoecium*, and found the process to take

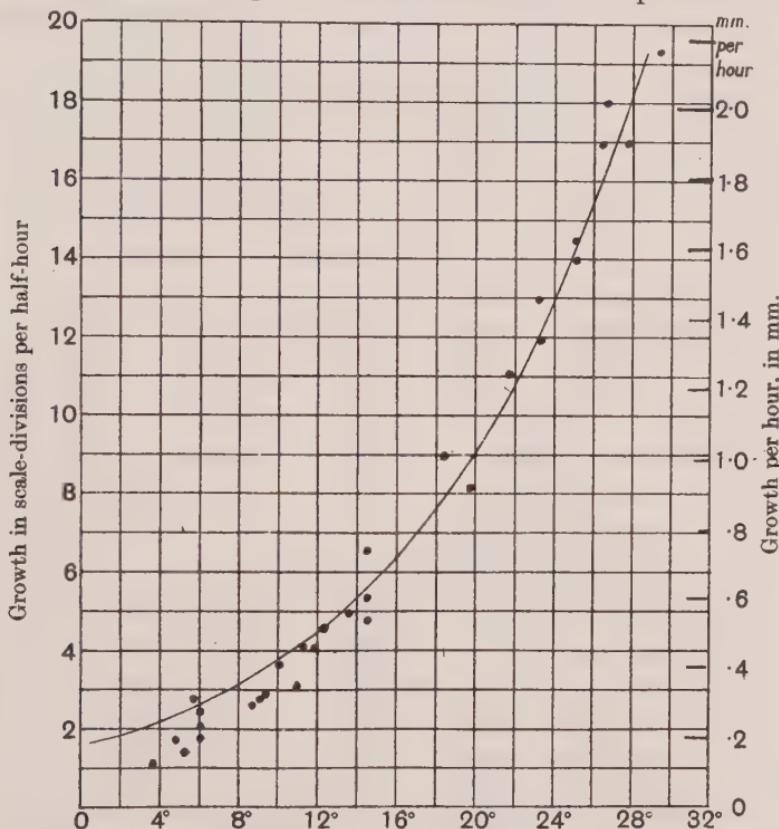


Fig. 64. Relation of rate of growth to temperature in rootlets of pea. From Miss I. Leitch's data.

29 minutes at 15°C ., 12 at 25° , and only 5 minutes at 35°C . These velocities are in the ratio of $1:2.4:5.76$, which ratio corresponds precisely to a temperature-coefficient of 2.4 for each rise of 10°C , or about 1.092 for each degree centigrade, precisely the same as we have found for the growth of the pea.

By means of this principle we may sometimes throw light on apparently complicated experiments. For instance, Fig. 65 is an

* Rec. de l'Inst. Bot. de Bruxelles, vi, 1906.

illustration, which has been often copied, of O. Hertwig's work on the effect of temperature on the rate of development of the tadpole*.

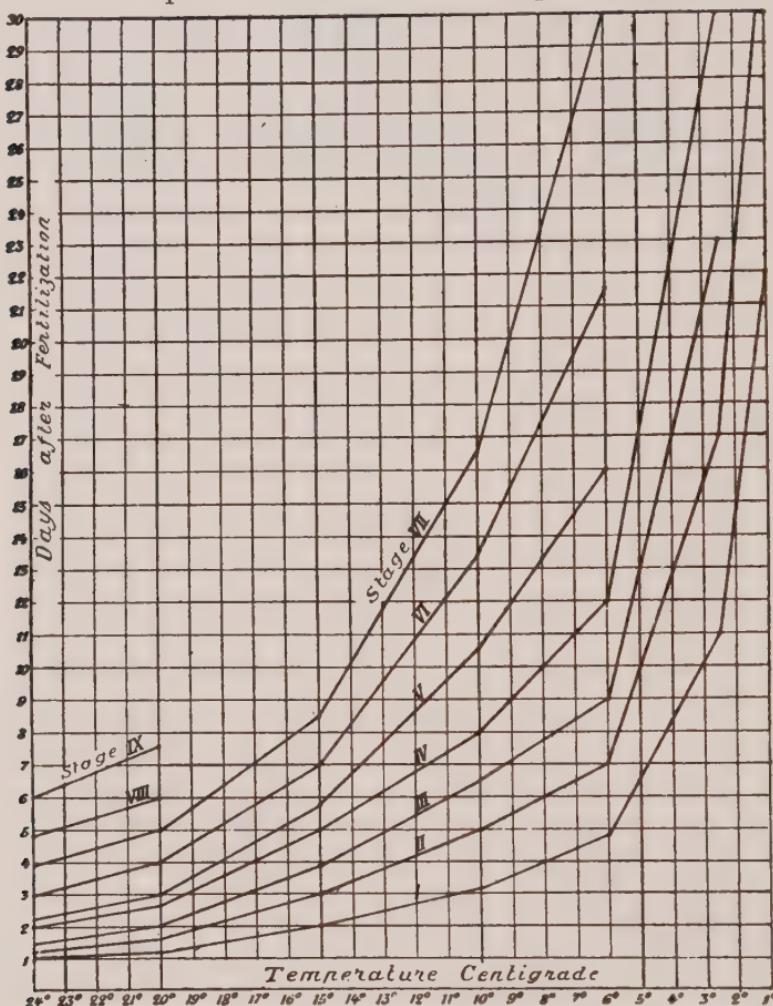


Fig. 65. Diagram shewing time taken (in days), at various temperatures ($^{\circ}$ C.), to reach certain stages of development in the frog: viz. I, gastrula; II, medullary plate; III, closure of medullary folds; IV, tail-bud; V, tail and gills; VI, tail-fin; VII, operculum beginning; VIII, do. closing; IX, first appearance of hind-legs. From Jenkinson, after O. Hertwig, 1898.

* O. Hertwig, Einfluss der Temperatur auf die Entwicklung von *Rana fusca* und *R. esculenta*, Arch. f. mikrosk. Anat. LI, p. 319, 1898. Cf. also K. Bialaszewicz, Beiträge z. Kenntniss d. Wachsthumsvorgänge bei Amphibienembryonen, Bull. Acad. Sci. de Cracovie, p. 783, 1908; Abstr. in Arch. f. Entwicklungsmech. XXVIII, p. 160, 1909: from which Ernst Cohen determined the value of Q_{10} (Vorträge üb. physikal. Chemie f. Ärzte, 1901; English edit. 1903).

From inspection of this diagram, we see that the time taken to attain certain stages of development (denoted by the numbers III-VII) was as follows, at 20° and at 10° C., respectively.

	At 20° C.	At 10° C.
Stage III	2.0	6.5 days
" IV	2.7	8.1 "
" V	3.0	10.7 "
" VI	4.0	13.5 "
" VII	5.0	16.8 "
Total	<u>16.7</u>	<u>55.6</u> "

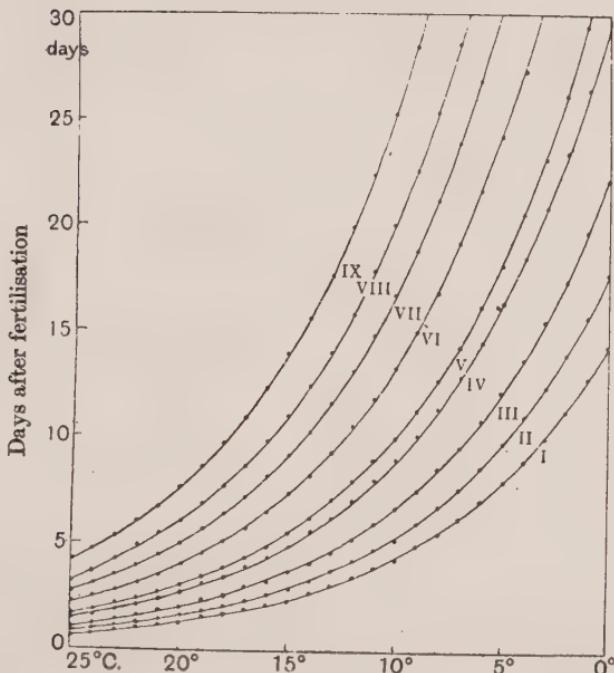


Fig. 66. Calculated values, corresponding to preceding figure.

That is to say, the time taken to produce a given result at 10° was (on the average) somewhere about $55.6/16.7$, or 3.33, times as long as was required at 20° C.

We may then put our equation in the simple form,

$$x^{10} = 3.33.$$

Or,

$$10 \log x = \log 3.33 = 0.52244.$$

Therefore

$$\log x = 0.05224,$$

and

$$x = 1.128.$$

That is to say, between the intervals of 10° and 20° C., if it take m days, at a certain given temperature, for a certain stage of development to be attained, it will take $m \times 1.128^n$ days, when the temperature is n degrees less, for the same stage to be arrived at.

Fig. 66 is calculated throughout from this value; and it will be found extremely concordant with the original diagram, as regards all the stages of development and the whole range of temperatures shewn; in spite of the fact that the coefficient on which it is based was derived by an easy method from a very few points on the original curves. In like manner, the following table shews the "incubation period" for trout-eggs, or interval between fertilisation and hatching, at different temperatures*:

Incubation-period of trout-eggs

Temperature ° C.	Days' interval before hatching
2.8	165
3.6	135
3.9	121
4.5	109
5.0	103
5.7	96
6.3	89
6.6	81
7.3	73
8.0	65
9.0	56
10.0	47
11.1	38
12.2	32

Choosing at random a pair of observations, viz. at 3.6° and 10° , and proceeding as before, we have

$$10^\circ - 3.6^\circ = 6.4^\circ.$$

Then $(6.4) = \frac{135}{47}$,

or $6.4 \times \log x = \log 135 - \log 47$
 $= 2.1303 - 1.6721 = 0.4582$

and $\log x = 0.4582 \div 6.4 = 0.0716$,
 $x = 1.179$.

* Data from James Gray, *The growth of fish, Journ. Exper. Biology*, vi, p. 126, 1928.

Using three other pairs of observations, we have the following concordant results:

At $12\cdot2^\circ$ and $2\cdot8^\circ$, $x = 1\cdot191$		
10·0°	3·6°	1·179
9·0°	5·7°	1·178
8·0°	5·0°	1·165 ..
		Mean 1·18

A very curious point is that (as Gray tells us) the young fish which have hatched slowly at a low temperature are bigger than those whose growth has been hastened by warmth.

Again, plaice-eggs were found to hatch and grow to a certain length (4·6 mm.), as follows*:

Temperature ($^\circ$ C.)	Days
4·1	23·0
6·1	18·1
8·0	13·3
10·1	10·3
12·0	8·3

From these we obtain, as before, the following constants:

At 12° and 8° , $x = 1\cdot13$		
12°	4·1°	1·14
10·1°	6·1°	1·15
8·0°	4·1°	1·15
		Mean 1·14

The value of x is much the same for the one fish as for the other.

Karl Peter†, experimenting on echinoderm eggs, and making use also of Richard Hertwig's experiments on young tadpoles, gives the temperature-coefficients for intervals of 10° C. (commonly written Q_{10}) as follows, to which I have added the corresponding values for Q_1 :

<i>Sphaerechinus</i>	$Q_{10} = 2\cdot15$	$Q_1 = 1\cdot08$
<i>Echinus</i>	2·13	1·08
<i>Rana</i>	2·86	1·11

* Data from A. C. Johansen and A. Krogh, Influence of temperature, etc., *Publ. de Circonstance*, No. 68, 1914. The function is here said to be a linear one—which would have been an anomalous and unlikely thing.

† Der Grad der Beschleunigung tierischer Entwicklung durch erhöhte Temperatur, *Arch. f. Entw. Mech.* xx, p. 130, 1905. More recently Bialaszewicz has determined the coefficient for the rate of segmentation in *Rana* as being 2·4 per 10° C.

These values are not only concordant, but are of the same order of magnitude as the temperature-coefficient in ordinary chemical reactions. Peter has also discovered the interesting fact that the temperature-coefficient alters with age, usually but not always decreasing as time goes on*:

<i>Sphaerechinus</i>	Segmentation	$Q_{10} = 2.29$	$Q_1 = 1.09$
	Later stages	2.03	1.07
<i>Echinus</i>	Segmentation	2.30	1.09
	Later stages	2.08	1.08
<i>Rana</i>	Segmentation	2.23	1.08
	Later stages	3.34	1.13

Furthermore, the temperature-coefficient varies with the temperature itself, falling as the temperature rises—a rule which Van't Hoff shewed to hold in ordinary chemical operations. Thus in *Rana* the temperature-coefficient (Q_{10}) at low temperatures may be as high as 5–6; which is just another way of saying that at low temperatures development is exceptionally retarded.

As the several stages of development are accelerated by warmth, so is the duration of each and all, and of life itself, proportionately curtailed. The span of life itself may have its temperature-coefficient—in so far as Life is a chemical process, and Death a chemical result. In hot climates puberty comes early, and old age (at least in women) follows soon; fishes grow faster and spawn earlier in the Mediterranean than in the North Sea. Jacques Loeb † found (in complete agreement with the general case) that the larval stages of a fly are abbreviated by rise of temperature; that the mean duration of life at various temperatures can be expressed by a temperature-coefficient of the usual order of magnitude; that this coefficient tends, as usual, to fall as the temperature rises; and lastly—what is not a little curious—that the coefficient is very much the same, in fact all but identical, for the larva, pupa and imago of the fly.

* The differences are, after all, of small order of magnitude, as is all the better seen when we reduce the ten-degree to one-degree coefficients.

† J. Loeb and Northrop, On the influence of food and temperature upon the duration of life, *Journ. Biol. Chemistry*, xxxii, pp. 103–121, 1917.

Temperature-coefficients (Q_{10}) of Drosophila

	Larva	Pupa	Imago
15–20° C.	1.15	1.17	1.18
20–25° C.	1.06	1.08	1.07

And Japanese students, studying a little fresh-water crustacean, have carried the experiment much beyond the range of Van't Hoff's law, and have found length of life to rise rapidly to a maximum at about 13–14° C., and to fall slowly, in a skew curve, thereafter* (Fig. 67).

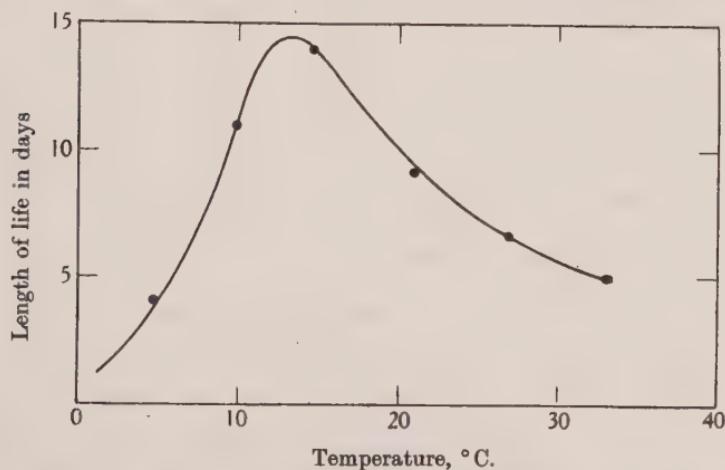


Fig. 67. Length of life, at various temperatures, in a water-flea.

If we now summarise the various temperature-coefficients (Q_1) which we have happened to consider, we are struck by their remarkably close agreement:

Yeast	$Q_1 = 1.13$
Lupin	1.16
Maize	1.20
Pea	1.09
Echinoids	1.08
<i>Drosophila</i> (mean)	1.12
Frog, segmentation	1.08
,, tadpole	1.13
Mean	<u>1.12</u>

* A. Terao and T. Tabaka, Duration of life in a water-flea, *Moina* sp.; *Journ. Imp. Fisheries Inst.*, Tokyo, xxv, No. 3, March 1930.

The constancy of these results might tempt us to look on the phenomenon as a simple one, though we well know it to be highly complex. But we had better rest content to see, as Arrhenius saw in the beginning, a general resemblance rather than an identity between the temperature-coefficients in physico-chemical and biological processes*.

It was seen from the first that to extend Van't Hoff's law from physical chemistry to physiology was a bold assumption, to all appearance largely justified, but always subject to severe and cautious limitations. If it seemed to simplify certain organic phenomena, further study soon shewed how far from simple these phenomena were. Living matter is always heterogeneous, and from one phase to another its reactions change; the temperature-coefficient varies likewise, and indicates at the best a summation, or integration, of phenomena. Nevertheless, attempts have been made to go a little further towards a physical explanation of the physiological coefficient. Van't Hoff suggested a viscosity-correction for the temperature-coefficient even of an ordinary chemical reaction; the viscosity of protoplasm varies in a marked degree, inversely with the temperature, and the viscosity-factor goes, perhaps, a long way to account for the aberrations of the temperature-coefficient. It has even been suggested (by Belehradek†) that the temperature-coefficients of the biologist are merely those of protoplasmic viscosity. For instance, the temperature-coefficients of mitotic cell-division have been shewn to alter from one phase to another of the mitotic process, being much greater at the start than at the end‡; and so, precisely, has it been shewn that protoplasmic viscosity is high at the beginning and low at the end of the mitotic process§.

On seasonal growth

There is abundant evidence in certain fishes, such as plaice and haddock, that the ascending curve of growth is subject to seasonal fluctuations or interruptions, the rate during the winter months being always slower than in the months of summer. Thus the Newfoundland cod have their maximum growth-rate in June, and in January–February they cease to grow; it is as though we superimposed a periodic annual sine-curve upon the continuous curve of growth. Furthermore, as growth itself grows less and less from year to year, so will the difference between the summer and the

* Cf. L. V. Heilbronn, *Science*, LXII, p. 268, 1925.

† J. Belehradek, in *Biol. Reviews*, v, pp. 30–58, 1930.

‡ Cf. E. Fauré-Fremiet, *La cinétique du développement*, 1925; also B. Ephrussi, *C.R. CLXXXII*, p. 810, 1926.

§ See (*int. al.*) L. V. Heilbronn, *The Colloid Chemistry of Protoplasm*, 1928.

winter rates grow less and less. The fluctuation in rate represents a vibration which is gradually dying out, the amplitude of the sine-curve diminishes till it disappears; in short our phenomenon is simply expressed by what is known as a "damped sine-curve*."

Growth in height of German military cadets, in half-yearly periods

Number observed	Age	Height (cm.)			Increment (cm.)		
		October	April	October	Winter $\frac{1}{2}$ -year	Summer $\frac{1}{2}$ -year	Year
12	11-12	139.4	141.0	143.3	1.6	2.3	3.9
80	12-13	143.0	144.5	147.4	1.5	2.9	4.4
146	13-14	147.5	149.5	152.5	2.0	3.0	5.0
162	14-15	152.2	155.0	158.5	2.8	3.5	6.3
162	15-16	158.5	160.8	163.8	2.3	3.0	5.3
150	16-17	163.5	165.4	167.7	1.9	2.3	4.2
82	17-18	167.7	168.9	170.4	1.2	1.5	2.7
22	18-19	169.8	170.6	171.5	0.8	0.9	1.7
6	19-20	170.7	171.1	171.5	0.4	0.4	0.8
		Mean			1.6	2.2	

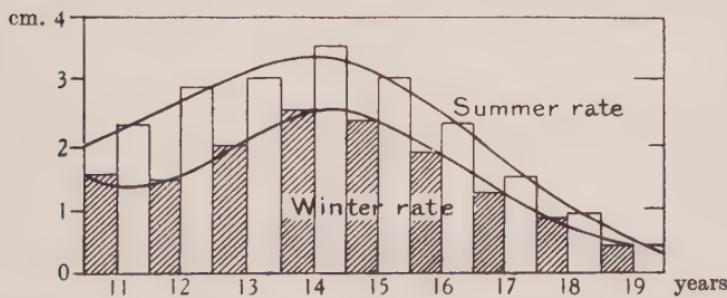


Fig. 68. Half-yearly increments of growth, in cadets of various ages.
From Daffner's data.

The same thing occurs in man, though neither in his case nor in that of the fish have we sufficient data for its complete illustration. We can demonstrate the fact, however, by help of certain measurements of the height of German cadets, measured at half-yearly intervals†. In the accompanying diagram (Fig. 68) the half-yearly increments are set forth from the above table, and it will be seen

* The scales, on the other hand, make most of their growth during the intermediate seasons: and with this peculiarity, that a few broad zones are added to the scale in spring, and a larger number of narrow circuli in autumn: see *Contrib. to Canadian Biology*, iv, pp. 289-305, 1929; Ben Dawes, Growth...in plaice, *Journ. M.B.A.* xvii, pp. 103-174, 1930.

† From Daffner, *Das Wachstum des Menschen*, p. 329. 1902.

that they form two even and entirely separate series. Danish schoolboys show just the same periodicity of growth in stature.

The seasonal effect on visible growth-rate is much alike in fishes and in man, in spite of the fact that the bodily temperature of the one varies with the *milieu externe* and that of the other keeps constant to within a fraction of a degree.

While temperature is the dominant cause, it is not the only cause of seasonal fluctuations of growth; for alternate scarcity and abundance of food is often, as in herbivorous animals, the ostensible

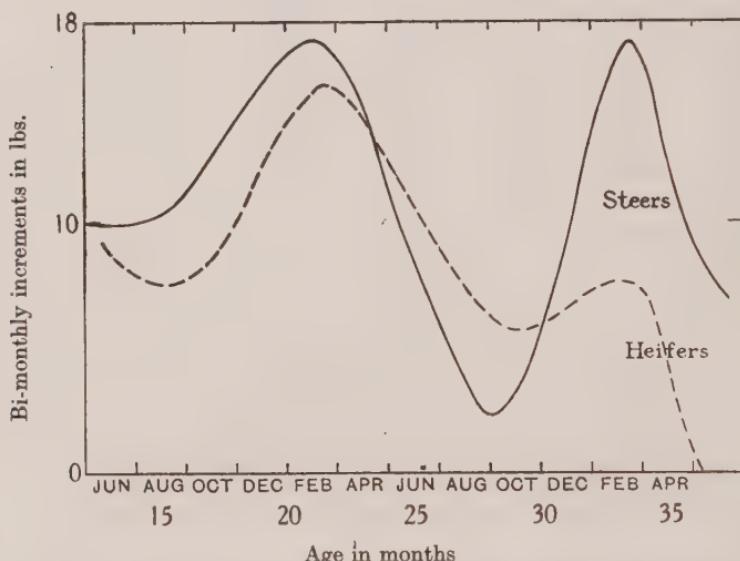


Fig. 69. Seasonal growth of S. African cattle: Sussex half-breeds.
After Schütte.

reason. Before turnips came into cultivation in the eighteenth century our own cattle starved for half the year and grew fat the other, and in many countries the same thing happens still. In South Africa the rainy season lasts from November to February; by January the grass is plentiful, by June or July the veldt is parched until rain comes again. Cattle fatten from January to March or April; from July to October they put on little weight, or lose weight rather than put it on*.

* Cf. D. J. Schütte, in *Onderstepoort Journal*, Oct. 1935.

The growth of trees

Some sixty years ago Sir Robert Christison, a learned and versatile Edinburgh professor, was the first to study the "exact measurement" of the girth of trees*; and his way of putting a girdle round the tree, and fitting a recording device to the girdle, is copied in the "dendrographs"† used in forestry today. The Edinburgh beeches begin to enlarge their trunks in late May or June, when in full leaf, and cease growing some three months later; the buds sprout and the leaves begin their work before the cambium wakens to activity. The beech-trees in Maryland do likewise, save that the dates are a little earlier in the year; and walnut-trees on high ground in Arizona shew a like short season of growth, differing somewhat in date or "phase," just as it did in Edinburgh, from one year to another.

Deciduous trees stop growing after the fall of the leaf, but evergreens grow all the year round, more or less. This broad fact is illustrated in the following table, which happens to relate to the

Mean monthly increase in girth of trees at San Jorge, Uruguay: from C. E. Hall's data. Values given in percentages of total annual increment‡

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Evergreens	9.1	8.8	8.6	8.9	7.7	5.4	4.3	6.0	9.1	11.1	10.8	10.2
Deciduous trees	20.3	14.6	9.0	2.3	0.8	0.3	0.7	1.3	3.5	9.9	16.7	21.0

southern hemisphere, and to the climate of Uruguay. The measurements taken were those of the girth of the tree, in mm., at three feet from the ground. The evergreens included *Pinus*, *Eucalyptus*

* Sir R. Christison, On the exact measurement of trees, *Trans. Edinb. Botan. Soc.* xiv, pp. 164–172, 1882. Cf. also Duhamel du Monceau, *Des semis, et plantation des arbres*, Paris, 1750. On the general subject see (*int. al.*) Pfeffer's *Physiology of Plants*, II, Oxford, 1906; A. Mallock, Growth of trees, *Proc. R.S.* (B), xc, pp. 186–191, 1919. Mallock used an exceedingly delicate optical method, in which interference-bands, produced by two contiguous glass plates, shew a visible displacement on the slightest angular movement of the plates, even of the order of a millionth of an inch.

† W. S. Glock, A. E. Douglass and G. A. Pearson, Principles... of tree-ring analysis, *Carnegie Inst. Washington*, No. 486, 1937; D. T. MacDougal, *Tree Growth*, Leiden, 1938, 240 pp.

‡ *Trans. Edinb. Botan. Soc.* xviii, p. 456, 1891.

and Acacia; the deciduous trees included Quercus, Populus, Robinia and Melia. The result (Fig. 70) is much as we might expect. The deciduous trees cease to grow in winter-time, and during all the months when the trees are bare; during the warm season the monthly values are regularly graded, approximately in a sine-curve, with a clear maximum (in the southern hemisphere) about the month of December. In the evergreens the amplitude of the

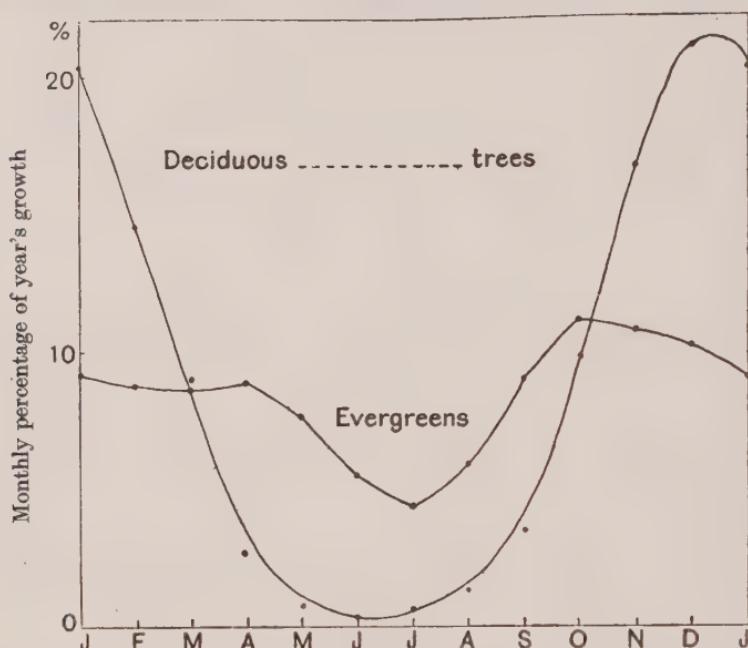


Fig. 70. Periodic annual fluctuation in rate of growth of trees in the southern hemisphere. From C. E. Hall's data.

annual wave is much less; there is a notable amount of growth all the year round, and while there is a marked diminution in rate during the coldest months, there is a tendency towards equality over a considerable part of the warmer season. In short, the evergreens, at least in this case, do not grow the faster as the temperature continues to rise; and it seems probable that some of them, especially the pines, are definitely retarded in their growth, either by a temperature above their optimum or by a deficiency of moisture, during the hottest season of the year.

Fig. 71 shews how a cypress never ceased to grow, but had alternate

spells of quicker and slower growth, according to conditions of which we are not informed. Another figure (Fig. 72) illustrates the growth in three successive seasons of the Californian redwood, a near ally of the most gigantic of trees. Evergreen though the redwood is, its growth has periods of abeyance; there is a second minimum about midsummer, and the chief maximum of the year may be that before or after this.

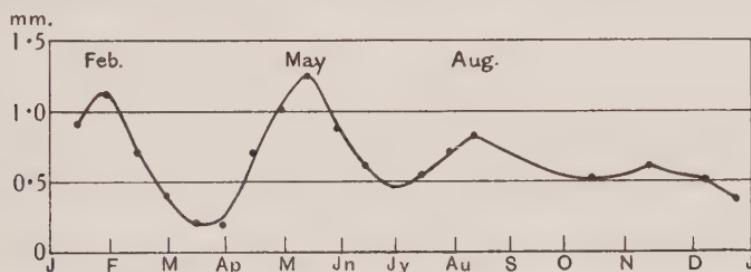


Fig. 71. Growth of cypress (*C. macrocarpa*), shewing seasonal periodicity.
From MacDougal's data: smoothed curve.

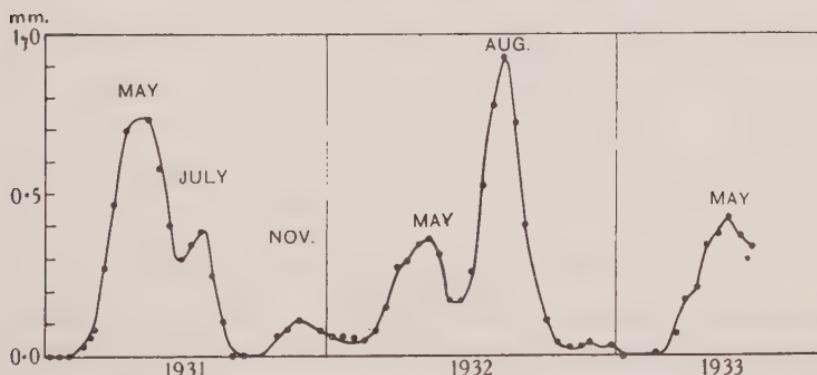


Fig. 72. Fortnightly increase of girth in Californian redwood (*Sequoia sempervirens*), shewing seasonal periodicity. After MacDougal.

In warm countries tree-growth is apt to shew a double maximum, for the cold of winter and the drought of summer are equally antagonistic to it. Trees grow slower—and grow fewer—the farther north we go, till only a few birches and willows remain, stunted and old; it is nearly a hundred years ago since Auguste Bravais* shewed a steadily decreasing growth-rate in the forests between 50° and 70° N.

* Recherches sur la croissance du pin silvestre dans le nord de l'Europe, *Mém. couronnées de l'Acad. R. de Belgique*, xv, 64 pp., 1840–41.

The delicate measuring apparatus now used shews sundry minor but beautiful phenomena. A daily periodicity of growth is a common thing* (Fig. 73). In the tree-cactuses the trunk expands by day and shrinks again after nightfall; for the stomata close in sunlight, and transpiration is checked until the sun goes down. But it is more usual for the trunk to shrink from sunrise until evening and to swell from sunset until dawn; for by daylight the leaves lose

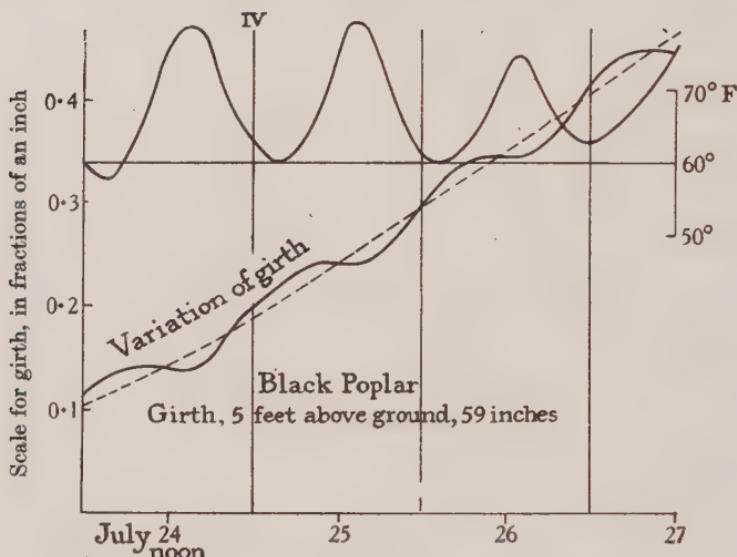


Fig. 73. Growth of black poplar, shewing daily periodicity.
After A. Mallock.

water faster, and in the dark they lose it slower, than the roots replace it. The rapid midday loss of water even at the top of a tall *Sequoia* is quickly followed by a measurable constriction of the trunk fifty or even a hundred yards below†.

* The diurnal periodicity is beautifully shewn in the case of the hop by Johannes Schmidt, *C.R. du Laboratoire Carlsberg*, x, pp. 235–248, Copenhagen, 1913.

† This rapid movement is accounted for by Dixon and Joly's "cohesion-theory" of the ascent of sap. The leaves shew innumerable minute menisci, or cup-shaped water-surfaces, in their intercellular air-spaces. As water evaporates from these the little cups deepen, capillarity increases its pull, and suffices to put in motion the strands or columns of water which run continuously through the vessels of wood, and withstand rupture even under a pull of 100–200 atmospheres. See (*int. al.*) H. H. Dixon and J. Joly, On the ascent of sap, *Phil. Trans. (B)*, clxxxvi, p. 563, 1895; also Dixon's *Transpiration and the Ascent of Sap*, 8vo, London, 1914.

In the case of trees, the seasonal periodicity of growth and the direct influence of weather are both so well marked that we are entitled to make use of the phenomenon in a converse way, and to draw deductions (as Leonardo da Vinci did*) as to climate during past years from the varying rates of growth which the tree has recorded for us by the thickness of its annual rings. Mr A. E. Douglass, of the University of California, has made a careful study of this question, and I received from him (through Professor H. H. Turner) some measurements of the average width of the annual rings in Californian redwood, five hundred years old, in which trees the rings are very clearly shewn. For the first hundred years the mean of two trees was used, for the next four hundred years the mean of five; and the means of these (and sometimes of larger numbers) were found to be very concordant. A correction was applied by drawing a nearly straight line through the curve for the whole period, which line was assumed to represent the slowly diminishing mean width of annual ring accompanying the increasing size, or age, of the tree; and the actual growth as measured was equated with this diminishing mean. The figures used give, then, the ratio of the actual growth in each year to the mean growth of the tree at that epoch.

It was at once manifest that the growth-rate so determined shewed a tendency to fluctuate in a long period of between 100 and 200 years. I then smoothed the yearly values in groups of 100 (by Gauss's method of "moving averages"), so that each number thus found represented the mean annual increase during a century: that is to say, the value ascribed to the year 1500 represented the *average annual growth* during the whole period between 1450 and 1550, and so on. These values, so simply obtained, give us a curve of beautiful and surprising smoothness, from which we draw the direct conclusion that the climate of Arizona, during the last five hundred years, has fluctuated with a regular periodicity of almost precisely 150 years. I have drawn, more recently, and also from Mr Douglass's data, a similar curve for a group of pine trees in Calaveras County†. These trees are about 300 years old, and the

* Cf. J. Playfair McMurrich, *Leonardo da Vinci*, 1930, p. 247.

† When this was first written I had not seen Mr Douglass's paper On a method of estimating rainfall by the growth of trees, *Bull. Amer. Geograph. Soc.* XLVI,

data are reduced, as before, to moving averages of 100 years, but without further correction. The agreement between the growth-rate of these pines and that of the great *Sequoias* during the same period is very remarkable (Fig. 74).

We should be left in doubt, so far as these observations go, whether the essential factor be a fluctuation of temperature or an alternation of drought and humidity; but the character of the Arizona climate, and the known facts of recent years, encourage the belief that the latter is the more direct and more important factor. In a New England forest many trees of many kinds were studied after a hurricane; they shewed on the whole no correlation

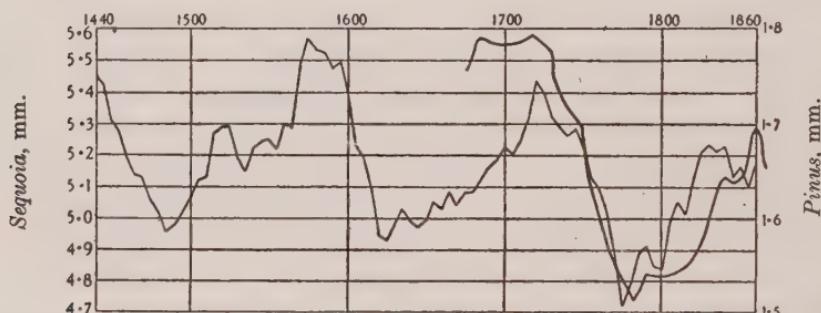


Fig. 74. Long-period fluctuation in growth of Arizona redwood (*Sequoia*), from A.D. 1390 to 1910; and of yellow pine from Calaveras County, from A.D. 1620 to 1920. (Smoothed in 100-year periods.)

between growth-rate and temperature, with the remarkable exception (in the conifers) of a clear correlation with the temperature of March and April, a month or two before the season's growth began. In a cold spring the melting snows and early rains ran off into the rivers, in a warm and early one they sank into the soil*; in other words, humidity was still the controlling factor. An ancient oak tree in Tunis is said to have recorded fifty years of abundant rain,

pp. 321-335, 1914; nor, of course, his great work on Climatic cycles and tree-growth, *Carnegie Inst. Publications*, 1919, 1928, 1936. Mr Douglass does not fail to notice the long period here described, but he is more interested in the sunspot-cycle and other shorter cycles known to meteorologists. See also (*int. al.*) E. Huntingdon, The fluctuating climate of North America, *Geograph. Journ.* Oct. 1912; and Otto Pettersson, Climatic variation in historic and prehistoric time, *Svenska Hydrografisk-Biolog. Skrifter*, v, 1914.

* C. J. Lyon, *Amer. Assoc. Rep.* 1939; *Nature*, Apr. 13, 1940, p. 595.

with short intervals of drought, during the eighteenth century; then, after 1790, longer droughts and shorter spells of rainy seasons*.

It has been often remarked that our common European trees, such as the elm or the cherry, have larger leaves the farther north we go; but the phenomenon is due to the longer hours of daylight throughout the summer, rather than to intensity of illumination or difference of temperature. On the other hand, long daylight, by prolonging vegetative growth, retards flowering and fruiting; and late varieties of soya bean may be forced into early ripeness by artificially shortening their daylight at midsummer†.

The effect of ultra-violet light, or any other portion of the spectrum, is part, and perhaps the chief part, of the same problem. That ultra-violet light accelerates growth has been shewn both in plants and animals‡. In tomatoes, growth is favoured by just such ultra-violet light as comes very near the end of the solar spectrum§, and as happens, also, to be especially absorbed by ordinary greenhouse glass||. At the other end of the spectrum, in red or orange light, the leaves become smaller, their petioles longer, the nodes more numerous, the very cells longer and more attenuated. It is a physiological problem, and as such it shews how plant-life is adapted, on the whole, to just such rays as the sun sends; but it also shews the morphologist how the secondary effects of climate may so influence growth as to modify both size and form¶. An analogous case is the influence of light, rather than temperature, in modifying the coloration of organisms, such as certain butterflies.

* Le chêne Zeem d'Ain Draham, *Bull. du Directeur Général*, Tunisie, 1927.

† That the plant grows by turns in darkness and in light, and has its characteristic growth-phases in each, longer or shorter according to species and variety and normal habitat, is a subject now studied under the name of "photoperiodism," and become of great practical importance for the northerly extension of cereal crops in Canada and Russia. Cf. R. G. Whyte and M. A. Oljovikov, *Nature*, Feb. 18, 1939.

‡ Cf. Kuro Suzuki and T. Hatano, in *Proc. Imp. Acad. of Japan*, III, pp. 94–96, 1927.

§ Withrow and Benedict, in *Bull. of Basic Scient. Research*, III, pp. 161–174, 1931.

|| Cf. E. C. Teodoresco, *Croissance des plantes aux lumières de diverses longueurs d'onde*, *Ann. Sc. Nat., Bot.* (8), pp. 141–336, 1929; N. Pfeiffer, *Botan. Gaz.* LXXXV, p. 127, 1929; etc.

¶ See D. T. MacDougal, *Influence of light and darkness, etc.*, *Mem. N.Y. Botan. Garden*, 1903, 392 pp.; *Growth in trees*, *Carnegie Inst.* 1921, 1924, etc.; J. Wiesner, *Lichtgenuss der Pflanzen*, VII, 322 pp., 1907; Earl S. Johnston, *Smithson. Misc. Contrib.* 18 pp., 1938; etc. On the curious effect of short spells of light and darkness, see H. Dickson, *Proc. R.S. (B)*, cxv, pp. 115–123, 1938.

Now if temperature or light affect the rate of growth in strict uniformity, alike in all parts and in all directions, it will only lead to local races or varieties differing in size, as the Siberian goldfinch or bullfinch differs from our own. But if there be ever so little of a discriminating tendency such as to enhance the growth of one tissue or one organ more than another*, then it must soon lead to racial, or even "specific," difference of form.

It is hardly to be doubted that climate has some such discriminating influence. The large leaves of our northern trees are an instance of it; and we have a better instance of it still in Alpine plants, whose general habit is dwarfed though their floral organs suffer little or no reduction†. Sunlight of itself would seem to be a hindrance rather than a stimulant to growth; and the familiar fact of a plant turning towards the sun means increased growth on the shady side, or partial inhibition on the other.

More curious and still more obscure is the moon's influence on growth, as on the growth and ripening of the eggs of oysters, sea-urchins and crabs. Belief in such lunar influence is as old as Egypt; it is confirmed and justified, in certain cases, nowadays, but the way in which the influence is exerted is quite unknown‡.

Osmotic factors in growth

The curves of growth which we have been studying have a twofold interest, morphological and physiological. To the morphologist, who has learned to recognise form as a "function of growth," the most important facts are these: (1) that rate of growth is an orderly phenomenon, with general features common to various organisms, each having its own characteristic rates, or specific constants; (2) that rate of growth varies with temperature, and so with season and with climate, and also with various other physical factors, external and internal to the organism; (3) that it varies in different parts of the body, and along various directions or axes:

* Or as we might say nowadays, have a different "threshold value" in one organ to another.

† Cf. for instance, Nägeli's classical account of the effect of change of habitat on alpine and other plants, *Sitzungsber. Baier. Akad. Wiss.* 1865, pp. 228-284.

‡ Cf. Munro Fox, Lunar periodicity in reproduction, *Proc. R.S. (B)*, xciv, pp. 523-550, 1935; also Silvio Ranzi, *Pubblic. Staz. Zool. Napoli*, xi, 1931.

such variations being harmoniously "graded," or related to one another by a "principle of continuity," so giving rise to the characteristic form and dimensions of the organism and to the changes of form which it exhibits in the course of its development. To the physiologist the phenomenon of growth suggests many other considerations, and especially the relation of growth itself to chemical and physical forces and energies.

To be content to shew that a certain rate of growth occurs in a certain organism under certain conditions, or to speak of the phenomenon as a "reaction" of the living organism to its environment or to certain stimuli, would be but an example of that "lack of particularity" with which we are apt to be all too easily satisfied. But in the case of growth we pass some little way beyond these limitations: to this extent, that an affinity with certain types of chemical and physical reaction has been recognised by a great number of physiologists*.

A large part of the phenomenon of growth, in animals and still more conspicuously in plants, is associated with "turgor," that is to say, is dependent on osmotic conditions. In other words, the rate of growth depends (as we have already seen) as much or more on the amount of water taken up into the living cells†, as on the actual amount of chemical metabolism performed by them; and sometimes, as in certain insect-larvae, we can even distinguish between tissues which grow by increase of cell-size, the result of imbibition, and others which grow by multiplication of their constituent cells‡. Of the chemical phenomena which result in the

* Cf. F. F. Blackman, Presidential Address in Botany, *Brit. Assoc.*, Dublin, 1908. The idea was first enunciated by Baudrimont and St Ange, *Recherches sur le développement du foetus*, *Mém. Acad. Sci.* xi, p. 469, 1851.

† Cf. J. Loeb, *Untersuchungen zur physiologischen Morphologie der Tiere*, 1892; also Experiments on cleavage, *Journ. Morphology*, vii, p. 253, 1892; Ueber die Dynamik des tierischen Wachstums, *Arch. f. Entw. Mech.* xv, p. 669, 1902-3; Davenport, On the rôle of water in growth, *Boston Soc. N.H.* 1897; Ida H. Hyde in *Amer. Journ. Physiology*, xii, p. 241, 1905; Bottazzi, Osmotischer Druck und elektrische Leistungsfähigkeit der Flüssigkeiten der Organismen, in Asher-Spiro's *Ergebnisse der Physiologie*, vii, pp. 160-402, 1908; H. A. Murray in *Journ. Gener. Physiology*, ix, p. 1, 1925; J. Gray, The role of water in the evolution of the terrestrial vertebrates, *Journ. Exper. Biology*, vi, pp. 26-31, 1928; and A. N. J. Heyn, Physiology of cell-elongation, *Botan. Review*, vi, pp. 515-574, 1940.

‡ Cf. C. A. Berger, Carnegie Inst. of Washington, *Contributions to Embryology*, xxvii, 1938.

actual increase of protoplasm we shall speak presently, but the rôle of water in growth deserves a passing word, even in our morphological enquiry.

The lower plants only live and grow in abundant moisture; few fungi continue growing when the humidity falls below 85 per cent. of saturation, and the mould-fungi, such as *Penicillium*, need more moisture still (Fig. 75). Their limit is reached a little below 90 %.

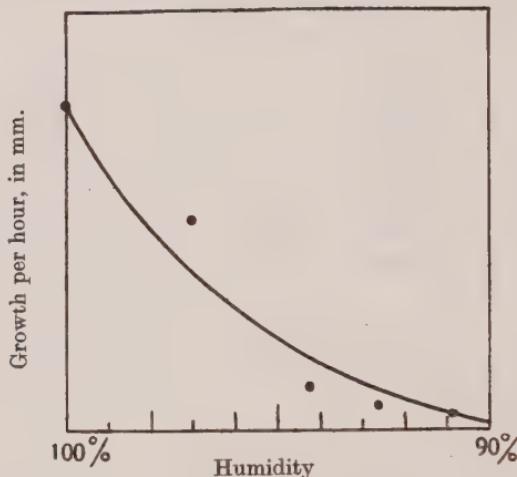


Fig. 75. Growth of *Penicillium* in relation to humidity.

*Growth of Penicillium (at 25° C.)**

Humidity (% of saturation)	Growth per hour (mm.)
100.0	7.7
97.0	5.0
94.2	1.0
92.6	0.5
90.8	0.3

Among the coelenterate animals growth and ultimate size depend on little more than absorption of water and consequent turgescence, the process shewing itself in simple ways. A sea-anemone may live to an immense age †, but its age and size have little to do with one

* From R. G. Tomkins, Studies of the growth of moulds, *Proc. R.S. (B)*, cv, pp. 375-401, 1929.

† Like Sir John Graham Dalyell's famous "Granny," and Miss Nelson's family of *Cereus* (not *Sagartia*) of which one still lives at over 80 years old. Cf. J. H. Ashworth and Nelson Annandale, in *Trans. R. Physical Soc. Edin.* xxv, pp. 1-14 1904.

another. It has an upper limit of size vaguely characteristic of the species, and if fed well and often it may reach it in a year; on stinted diet it grows slowly or may dwindle down; it may be kept at wellnigh what size one pleases. Certain full-grown anemones were left untended in war-time, unfed and in water which evaporated down to half its bulk; they shrank down to little beads, and grew up again when fed and cared for.

Loeb shewed, in certain zoophytes, that not only must the cells be turgescent in order to grow, but that this turgescence is possible only so long as the salt-water in which the cells lie does not overstep a certain limit of concentration: a limit reached, in the case of *Tubularia*, when the salinity amounts to about 3·4 per cent. Seawater contains some 3·0 to 3·5 per cent. of salts in the open sea, but the salinity falls much below this normal, to about 2·2 per cent., before *Tubularia* exhibits its full turgescence and maximal growth; a further dilution is deleterious to the animal. It is likely enough that osmotic conditions control, after this fashion, the distribution and local abundance of many zoophytes. Loeb has also shewn* that in certain fish-eggs (e.g. of *Fundulus*) an increasing concentration, leading to a lessening water-content of the egg, retards the rate of segmentation and at last arrests it, though nuclear division goes on for some time longer.

The eggs of many insects absorb water in large quantities, even doubling their weight thereby, and fail to develop if drought prevents their doing so; and sometimes the egg has a thin-walled stalk, or else a "hydropyle." or other structure by which the water is taken in†.

In the frog, according to Bialaszewicz ‡, the growth of the embryo while within the vitelline membrane depends wholly on absorption of water. The rate varies with the temperature, but the amount of water absorbed is constant, whether growth be fast or slow. Moreover, the successive changes of form correspond to definite quantities of water absorbed, much of which water is intracellular. The solid residue, as Davenport has also shewn, may even diminish

* *Pflüger's Archiv*, LV, 1893.

† Cf. V. B. Wigglesworth, *Insect Physiology*, 1939, p. 2.

‡ Beiträge zur Kenntniss d. Wachstumsvorgänge bei Amphibienembryonen, *Bull. Acad. Sci. de Cracovie*, 1908, p. 783; also A. Drzwina and C. Bohn, De l'action... des solutions salines sur les larves des batraciens, *ibid.* 1906.

notably, while all the while the embryo continues to grow in bulk and weight. But later on, and especially in the higher animals, the water-content diminishes as growth proceeds and age advances; and loss of water is followed, or accompanied, by retardation and cessation of growth. A crab loses water as each phase of growth draws to an end and the corresponding moult approaches; but it absorbs water in large quantities as soon as the new period of growth begins*. Moreover, that water is lost as growth goes on has been shewn by Davenport for the frog, by Potts for the chick, and particularly by Fehling in the case of man. Fehling's results may be condensed as follows:

Age in weeks (man)	6	17	22	24	26	30	35	39
Percentage of water	97.5	91.8	92.0	89.9	86.4	83.7	82.9	74.2

The following illustrate Davenport's results for the frog:

Age in weeks (frog)	1	2	5	7	9	14	41	84
Percentage of water	56.3	58.5	76.7	89.3	93.1	95.0	90.2	87.5

The following table epitomises the drying-off of ripening maize†; it shews how ripening and withering are closely akin, and are but two phases of senescence (Fig. 76):

Days (from August 6)	0	22	35	49	56	63
Percentage of water	87	81	77	68	65	58

The bird's egg provides all the food and all the water which the growing embryo needs, and to carry a provision of water is the special purpose of the white of the egg; the water contained in the albumen at the beginning of incubation is just about what the chick contains at the end. The yolk is not surrounded by water, which would diffuse too quickly into it, nor by a crystalloid solution, whose osmotic value would soon increase; but by a watery albuminous colloid, whose osmotic pressure changes slowly as its charge of water is gradually withdrawn‡.

* Cf. A. Krogh, *Osmotic regulation in aquatic animals*, Cambridge, 1939.

† Henry and Morrison, 1917; quoted by Otto Glaser, on Growth, time and form, *Biolog. Reviews*, XIII, pp. 2-58, 1938.

‡ Cf. James Gray, in *Journ. Exper. Biology*, IV, pp. 214-225, 1926.

Distribution of water in a hen's egg

Day of incubation	Gm. of water contained in			Loss by evaporation	Gain by combustion
	Albumen	Embryo	Yolk		
0	29.9	0.0	8.5	0.0	0.0
6	27.2	0.4	8.45	2.4	0.01
12	20.4	4.6	7.8	5.6	0.27
18	9.2	18.1	2.3	8.8	1.20
20	2.2	27.4	1.0	9.8	2.00

The actual amount of water, compared with the dry solids in the egg, has been determined as follows:

Day of incubation (chick)	5	8	11	14	17	19
Percentage of water	94.7	93.8	92.3	87.7	82.8	82.3

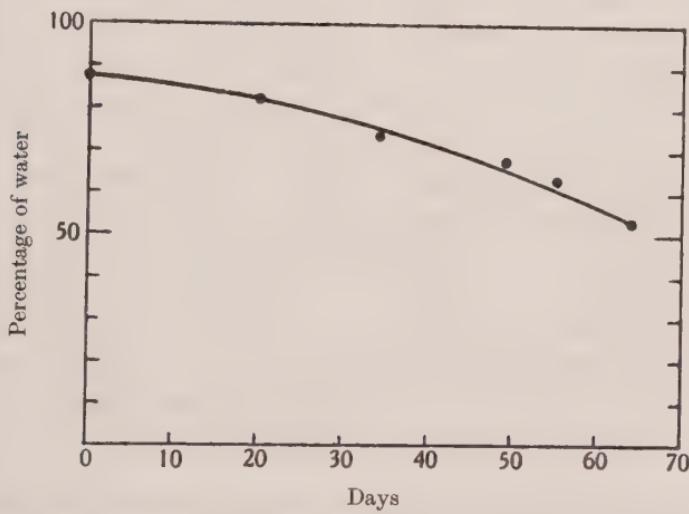


Fig. 76. Percentage of water in ripening maize. From Otto Glaser.

We know very little of the part which all this water plays: how much is mere "reaction-medium," how much is fixed in hydrated colloids, how much, in short, is bound or unbound. But we see that somehow or other water is lost, and lost in considerable amount, as the embryo draws towards completion and ceases for the time being to grow.

All vertebrate animals contain much the same amount of water in their living bodies, say 85 per cent. or thereby, however unequally

distributed in the tissues that water may be*. Land animals have evolved from water animals with little change in this respect, though the constant proportion of water is variously achieved. A newt loses moisture by evaporation with the utmost freedom, and regains it by no less rapid absorption through the skin; while a lizard in his scaly coat is less liable to the one and less capable of the other, and must drink to replace what water it may lose.

We are on the verge of a difficult subject when we speak of the rôle of water in the living tissues, in the growth of the organism, and in the manifold activities of the cell; and we soon learn, among other more or less unexpected things, that osmotic equilibrium is neither universal nor yet common in the living organism. The yolk maintains a higher osmotic pressure than the white of the egg—so long as the egg is living; and the watery body of a jellyfish, though not far off osmotic equilibrium, has a somewhat less salinity than the sea-water. In other words, its surface acts to some extent as a semipermeable membrane, and the fluid which causes turgescence of the tissues is less dense than the sea-water outside†.

In most marine invertebrates, however, the body-fluids constituting the *milieu interne* are isotonic with the *milieu externe*, and vary in these animals *pari passu* with the large variations to which sea-water itself is subject. On the other hand, the dwellers in fresh-water, whether invertebrates or fishes, have, naturally, a more concentrated medium within than without. As to fishes, different kinds shew remarkable differences. Sharks and dogfish have an osmotic pressure in their blood and their body fluids little different

* The vitreous humour is nearly all water, the enamel has next to none, the grey matter has some 86 per cent., the bones, say 22 per cent.; lung and kidney take up more than they can hold, and so become excretory or regulatory organs. Eggs, whether of dogfish, salmon, frogs, snakes or birds, are composed, roughly speaking, of half water and half solid matter.

† Cf. (*int. al.*) G. Teissier, Sur la teneur en eau...de Chrysaora, *Bull. Soc. Biol. de France*, 1926, p. 266. And especially A. V. Hill, R. A. Gortner and others, On the state of water in colloidal and living systems, *Trans. Faraday Soc.* xxvi, pp. 678–704, 1930. For recent literature see (e.g.) Homer Smith, in *Q. Rev. Biol.* vii, p. 1, 1932; E. K. Marshall, *Physiol. Rev.* xiv, p. 133, 1934; Lovatt Evans, *Recent Advances in Physiology*, 4th ed., 1930; M. Duval, Recherches...sur le milieu intérieur des animaux aquatiques, *Thèse*, Paris, 1925; Paul Portier, *Physiologie des animaux marins*, Chap. III, Paris, 1938; G. P. Wells and I. C. Ledingham, Effects of a hypotonic environment, *Journ. Exp. Biol.* xvii, pp. 337–352, 1940.

from that of the sea-water outside: but with certain chemical differences, for instance that the chlorides within are much diminished, and the molecular concentration is eked out by large accumulations of urea in the blood. The marine teleosts, on the other hand, have a much lower osmotic pressure within than that of the sea-water outside, and only a little higher than that of their fresh-water allies. Some, like the conger-eel, maintain an all but constant internal concentration, very different from that outside; and this fish, like others, is constantly absorbing water from the sea; it must be exuding or excreting salt continually*. Other teleosts differ greatly in their powers of regulation and of tolerance, the common stickleback (which we may come across in a pool or in the middle of the North Sea) being exceptionally tolerant or "euryhaline†." Physiology becomes "comparative" when it deals with differences such as these, and Claude Bernard foresaw the existence of just such differences: "Chez tous les êtres vivants le milieu intérieur, qui est un produit de l'organisme, conserve les rapports nécessaires d'échange avec le milieu extérieur; mais à mesure que l'organisme devient plus parfait *le milieu organique se spécifie*, et s'isole en quelque sorte de plus en plus au milieu ambiant‡." Claude Bernard was building, if I mistake not, on Bichat's earlier concept, famous in its day, of life as "une alternation habituelle d'action de la part des corps extérieurs, et de réaction de la part du corps vivant": out of which grew his still more famous aphorism, "La vie est l'ensemble des fonctions qui résistent à la mort§."

One crab, like one fish, differs widely from another in its power

* Probably by help of Henle's tubules in the kidney, which structures the dogfish does not possess. But the gills have their part to play as water-regulators, as also, for instance, in the crab.

† The grey mullets go down to the sea to spawn, but may live and grow in brackish or nearly fresh-water. The several species differ much in their adaptability, and Brunelli sets forth, as follows, the range of salinity which each can tolerate:

<i>M. auratus</i>	24-35 per mille
<i>saliens</i>	16-40
<i>chelo</i>	10-40
<i>capito</i>	5-40
<i>cephalus</i>	4-40

‡ *Introduction à l'étude de la médecine expérimentale*, 1855, p. 110. For a discussion of this famous concept see J. Barcroft, "La fixité du milieu intérieur est la condition de la vie libre," *Biol. Reviews*, VIII, pp. 24-87, 1932.

§ *Sur la vie et la mort*, p. 1.

of self-regulation; and these physiological differences help to explain, in both cases, the limitation of this species or that to more or less brackish, or more or less saline, waters. In deep-sea crabs (*Hyas*, for instance) the osmotic pressure of the blood keeps nearly to that of the *milieu externe*, and falls quickly and dangerously with any dilution of the latter; but the little shore-crab (*Carcinus moenas*) can live for many days in sea-water diluted down to one-quarter of its usual salinity. Meanwhile its own fluids dilute slowly, but not near so far; in other words, this crab combines great powers of osmotic regulation with a large capacity for tolerating osmotic gradients which are beyond its power to regulate. How the unequal balance is maintained is yet but little understood. But we do know that certain organs or tissues, especially the gills and the antennary gland, absorb, retain or eliminate certain elements, or certain ions, faster than others, and faster than mere diffusion accounts for; in other words, "ionic" regulation goes hand in hand with "osmotic" regulation, as a distinct and even more fundamental phenomenon*. This at least seems generally true—and only natural—that quickened respiration and increased oxygen-consumption accompany all such one-sided conditions: in other words, the "steady state" is only maintained by the doing of work and the expenditure of energy†.

To the dependence of growth on the uptake of water, and to the phenomena of osmotic balance and its regulation, Höber‡ and also Loeb were inclined to refer the modifications of form which certain phyllopod crustacea undergo when the highly saline waters which they inhabit are further concentrated, or are abnormally diluted. Their growth is retarded by increased concentration, so that individuals from the more saline waters appear stunted and dwarfish; and they become altered or transformed in other ways, suggestive of "degeneration," or a failure to attain full and perfect develop-

* See especially D. A. Webb, Ionic regulation in *Carcinus moenas*, *Proc. R.S. (B)*, cxxix, pp. 107–136, 1940.

† In general the fresh-water Crustacea have a larger oxygen-consumption than the marine. *Stenohaline* and *euryhaline* are terms applied nowadays to species which are confined to a narrow range of salinity, or are tolerant of a wide one. An extreme case of toleration, or adaptability, is that of the Chinese woolly-handed crab, *Eriocheir*, which has not only acclimatised itself in the North Sea but has ascended the Elbe as far as Dresden.

‡ R. Höber, Bedeutung der Theorie der Lösungen für Physiologie und Medizin, *Biol. Centralbl.* xix, p. 272, 1899.

ment*. Important physiological changes ensue. The consumption of oxygen increases greatly in the stronger brines, as more and more active "osmo-regulation" is required. The rate of multiplication is increased, and parthenogenetic reproduction is encouraged. In the less saline waters male individuals, usually rare, become plentiful, and here the females bring forth their young alive; males disappear altogether in the more concentrated brines, and then the females lay eggs, which, however, only begin to develop when the salinity is somewhat reduced.

The best-known case is the little brine-shrimp, *Artemia salina*, found in one form or another all the world over, and first discovered nearly two hundred years ago in the salt-pans at Lymington. Among many allied forms, one, *A. milhausenii*, inhabits the natron-lakes of Egypt and Arabia, where, under the name of "loul," or "Fezzan-worm," it is eaten by the Arabs†. This fact is interesting, because it indicates (and investigation has apparently confirmed) that the tissues of the creature are not impregnated with salt, as is the medium in which it lives. In short *Artemia*, like teleostean fishes in the sea, lives constantly in a "hypertonic medium"; the fluids of the body, the *milieu interne*, are no more salt than are those of any ordinary crustacean or other animal, but contain only some 0·8 per cent. of NaCl‡, while the *milieu externe* may contain from 3 to 30 per cent. of this and other salts; the skin, or body-wall, of the creature acts as a "semi-permeable membrane," through which the dissolved salts are not permitted to diffuse, though water passes freely. When brought into a lower concentration the animal may grow large and turgescent, until a statical equilibrium, or steady state, is at length attained.

Among the structural changes which result from increased con-

* Schmankewitsch, *Zeitschr. f. wiss. Zool.* xxix, p. 429, 1877. Schmankewitsch has made equally interesting observations on change of size and form in other organisms, after some generations in a milieu of altered density; e.g. in the flagellate infusorian *Ascinonema acinus* Bütschli.

† These "Fezzan-worms," when first described, were supposed to be "insects' eggs"; cf. Humboldt, *Personal Narrative*, vi, i, 8, note; Kirby and Spence, Letter x.

‡ See D. J. Kuenen, Notes, systematic and physiological, on *Artemia*, *Arch. Néerland. Zool.* iii, pp. 365–449, 1939; cf. also Abonyi, *Z. f. w. Z.* cxiv, p. 134, 1915. Cf. Mme. Medwedewa, Ueber den osmotischen Druck der Haemolymph v. *Artemia*; in *Ztsch. f. vergl. Physiolog.* v, pp. 547–554, 1922.

centration of the brine (partly during the life-time of the individual, but more markedly during the short season which suffices for the development of three or four, or perhaps more, successive generations), it is found that the tail comes to bear fewer and fewer bristles, and the tail-fins themselves tend at last to disappear: these changes corresponding to what have been described as the specific characters of *A. milhausenii*, and of a still more extreme form, *A. köppeniana*; while on the other hand, progressive dilution of the water tends to precisely opposite conditions, resulting in forms which have also been described as separate species, and even

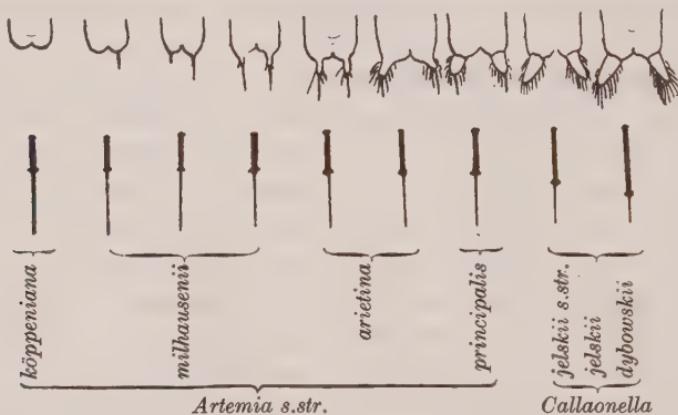


Fig. 77. Brine-shrimps (*Artemia*), from more or less saline water. Upper figures shew tail-segment and tail-fins; lower figures, relative length of cephalothorax and abdomen. After Abonyi.

referred to a separate genus, *Callaonella*, closely akin to *Branchipus* (Fig. 77). *Pari passu* with these changes, there is a marked change in the relative lengths of the fore and hind portions of the body, that is to say, of the cephalothorax and abdomen: the latter growing relatively longer, the salter the water. In other words, not only is the rate of growth of the whole animal lessened by the saline concentration, but the specific rates of growth in the parts of its body are relatively changed. This latter phenomenon lends itself to numerical statement, and Abonyi has shewn that we may construct a very regular curve, by plotting the proportionate length of the creature's abdomen against the salinity, or density, of the water; and the several species of *Artemia*, with all their other correlated specific characters, are then found to occupy successive, more or less well-defined, and more or less extended, regions of the

curve (Fig. 78). In short, the density of the water is so clearly "specific," that we might briefly define *Artemia jelskii*, for instance, as the *Artemia* of density 1000–1010 (NaCl), or all but fresh water, and the typical *A. salina* (or *principalis*) as the *Artemia* of density 1018–1025, and so on*.

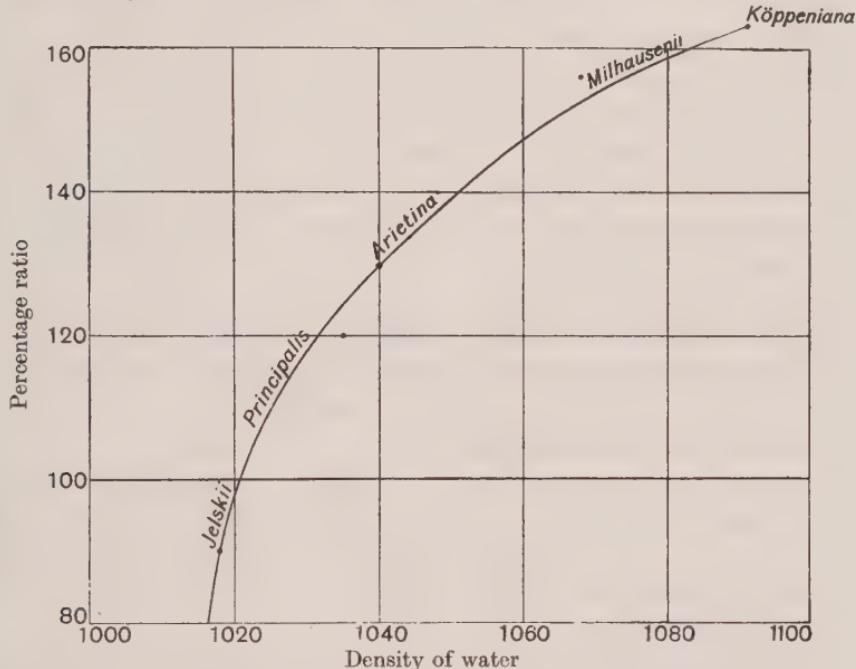


Fig. 78. Percentage ratio of length of abdomen to cephalothorax in brine-shrimps, at various salinities. After Abonyi.

These Artemiae are capable of living in waters not only of great density, but of very varied chemical composition, and it is hard to say how far they are safeguarded by semi-permeability or by specific properties and reactions of the living colloids†. The natron-lakes,

* Different authorities have recognised from one to twenty species of *Artemia*. Daday de Deés (*Ann. sci. nat.* 1910) reduces the salt-water forms to one species with four varieties, but keeps *A. jelskii* in a separate sub-genus. Kuenen suggests two species, *A. salina* and *gracilis*, one for the European and one for the American forms. According to Schmanekewitsch every systematic character can be shewn to vary with the external medium. Cf. Professor Labbé on change of characters, specific and even generic, of Copepods according to the pH of saline waters at Le Croisic, *Nature*, March 10, 1928.

† We may compare Wo. Ostwald's old experiments on *Daphnia*, which died in a pure solution of NaCl isotonic with normal sea-water. Their death was not to be explained on osmotic grounds; but was seemingly due to the fact that the organic gels do not retain their normal water-content save in the presence of such concentrations of MgCl₂ (and other salts) as are present in sea-water.

for instance, contain large quantities of magnesium sulphate; and the *Artemiae* continue to live equally well in artificial solutions where this salt, or where calcium chloride, has largely replaced the common salt of the more usual habitat. Moreover, such waters as those of the natron-lakes are subject to great changes of chemical composition as evaporation and concentration proceed, owing to the different solubilities of the constituent salts; but it appears that the forms which the *Artemiae* assume, and the changes which they undergo, are identical, or indistinguishable, whichever of the above salts happen to exist or to predominate in their saline habitat. At the same time we still lack, so far as I know, the simple but crucial experiments which shall tell us whether, in solutions of different chemical composition, it is *at equal densities*, or *at isotonic concentrations* (that is to say, under conditions where the osmotic pressure, and consequently the rate of diffusion, is identical), that the same changes of form and structure are produced and corresponding phases of equilibrium attained.

Sea-water has been described as an instance of the "fitness of the environment*" for the maintenance of protoplasm in an appropriate milieu; but our *Artemias* suffice to shew how nature, when hard put to it, makes shift with an environment which is wholly abnormal and anything but "fit."

While Höber and others† have referred all these phenomena to osmosis, Abonyi is inclined to believe that the viscosity, or mechanical resistance, of the fluid also reacts upon the organism; and other possible modes of operation have been suggested. But we may take it for certain that the phenomenon as a whole is not a simple one. We should have to look far in organic nature for what the physicist would call simple osmosis‡; and assuredly there is always at work, besides the passive phenomena of intermolecular

* L. H. Henderson, *The Fitness of the Environment*, 1913.

† Cf. Schmankewitsch, *Z. f. w. Zool.* xxv, 1875; xxix, 1877, etc.; transl. in appendix to Packard's *Monogr. of N. American Phyllopoda*, 1883, pp. 466–514; Daday de Deés, *Ann. Sci. Nat. (Zool.)*, (9), xi, 1910; Samter und Heymons, *Abh. d. K. pr. Akad. Wiss.* 1902; Bateson, *Mat. for the Study of Variation*, 1894, pp. 96–101; Anikin, *Mitth. Kais. Univ. Tomsk*, xiv: *Zool. Centralbl.* vi, pp. 756–760, 1908; Abonyi, *Z. f. w. Zool.* cxiv, pp. 96–168, 1915 (with copious bibliography), etc.

‡ Cf. C. F. A. Pantin, *Body fluids in animals*, *Biol. Reviews*, vi, p. 4, 1931; J. Duclaux, *Chimie appliquée à la biologie*, 1937, ii, chap. 4.

diffusion, some other activity to play the part of a regulatory mechanism*.

On growth and catalytic action

In ordinary chemical reactions we have to deal (1) with a specific velocity proper to the particular reaction, (2) with variations due to temperature and other physical conditions, (3) with variations due to the quantities present of the reacting substances, according to Van't Hoff's "Law of Mass Action," and (4) in certain cases with variations due to the presence of "catalysing agents," as Berzelius called them a hundred years ago†. In the simpler reactions, the law of mass involves a steady slowing-down of the process as the reaction proceeds and as the initial amount of substance diminishes: a phenomenon, however, which is more or less evaded in the organism, part of whose energies are devoted to the continual bringing-up of supplies.

Catalytic action occurs when some substance, often in very minute quantity, is present, and by its presence produces or accelerates a reaction by opening "a way round," without the catalysing agent itself being diminished or used up‡. It diminishes the resistance somehow—little as we know what resistance means

* According to the empirical canon of physiology, that, as Léon Frédéricq expresses it (*Arch. de Zool.* 1885), "L'être vivant est agencé de telle manière que chaque influence perturbatrice provoque d'elle-même la mise en activité de l'appareil compensateur qui doit neutraliser et réparer le dommage." Herbert Spencer had conceived a similar principle, and thought he recognised in it the *vis medicatrix Naturae*. It is the physiological analogue of the "principle of Le Chatelier" (1888), with this important difference that the latter is a rigorous and quantitative law, based on a definite and stable equilibrium. The close relation between the two is maintained by Le Dantec (*La Stabilité de la Vie*, 1910, p. 24), and criticised by Lotka (*Physical Biology*, p. 283 seq.).

† In a paper in the *Berliner Jahrbuch* for 1836. This paper was translated in the *Edinburgh New Philosophical Journal* in the following year; and a curious little paper On the coagulation of albumen, and catalysis, by Dr Samuel Brown, followed in the *Edinburgh Academic Annual* for 1840.

‡ Such phenomena come precisely under the head of what Bacon called *Instances of Magic*: "By which I mean those wherein the material or efficient cause is scanty and small as compared with the work or effect produced; so that even when they are common, they seem like miracles, some at first sight, others even after attentive consideration. These magical effects are brought about in three ways...[of which one is] by excitation or invitation in another body, as in the magnet which excites numberless needles without losing any of its virtue, or in yeast and such-like." *Nov. Org.*, cap. li.

in a chemical reaction. But the velocity-curve is not altered in form; for the amount of energy in the system is not affected by the presence of the catalyst, the law of mass exerts its effect, and the rate of action gradually slows down. In certain cases we have the remarkable phenomenon that a body capable of acting as a catalyser is necessarily formed as a product, or by-product, of the main reaction, and in such a case as this the reaction-velocity will tend to be steadily accelerated. Instead of dwindling away, such a reaction continues with an ever-increasing velocity: always subject to the reservation that limiting conditions will in time make themselves felt, such as a failure of some necessary ingredient (the "law of the minimum"), or the production of some substance which shall antagonise and finally destroy the original reaction. Such an action as this we have learned, from Ostwald, to describe as "autocatalysis." Now we know that certain products of protoplasmic metabolism—we call them enzymes—are very powerful catalysers, a fact clearly understood by Claude Bernard long ago*; and we are therefore entitled, to that extent, to speak of an autocatalytic action on the part of protoplasm itself.

Going a little farther in the footsteps of Claude Bernard, Chodat of Geneva suggested (as we are told by his pupil Monnier) that growth itself might be looked on as a catalytic, or autocatalytic reaction: "On peut bien, ainsi que M. Chodat l'a proposé, considérer l'accroissement comme une réaction chimique complexe, dans laquelle le catalysateur est la cellule vivante, et les corps en présence sont l'eau, les sels et l'acide carbonique†."

A similar suggestion was made by Loeb, in connection with the

* "Les diastases contiennent, en définitive, le secret de la vie. Or, les actions diastatiques nous apparaissent comme des phénomènes catalytiques; en d'autres termes, des accélérations de vitesse de réaction." Cf. M. F. Porchet, *Revue Scientifique*, 18th Feb. 1911. For a last word on this subject, see W. Frankenberger, *Katalytische Umsetzungen in homogenen u. enzymatischen Systemen*, Leipzig, 1937.

† Cf. R. Chodat, *Principes de Botanique* (2nd ed.), 1907, p. 133; A. Monnier, La loi d'accroissement des végétaux, *Publ. de l'Inst. de Bot. de l'Univ. de Genève* (7), III, 1905. Cf. W. Ostwald, *Vorlesungen über Naturphilosophie*, 1902, p. 342; Wo. Ostwald, Zeitliche Eigenschaften der Entwicklungsvorgänge, in Roux's *Vorträge*, Heft 5, 1908; Robertson, Normal growth of an individual, and its biochemical significance, *Arch. f. Entw. Mech.* xxv, pp. 581-614; xxvi, pp. 108-118, 1908; S. Hatai, Growth-curves from a dynamical standpoint, *Anat. Record*, v, p. 373, 1911; A. J. Lotka, *Ztschr. f. physikal. Chemie*, LXXII, p. 511, 1910; LXXX, p. 159, 1912; etc.

synthesis of nuclear protoplasm, or *nuclein*; for he remarked that, as in an autocatalysed chemical reaction, the rate of synthesis increases during the initial stage of cell-division in proportion to the amount of nuclear matter already there. In other words, one of the products of the reaction, i.e. one of the constituents of the nucleus, accelerates the production of nuclear from cytoplasmic material. To take one more instance, Blackman said, in the address already quoted, that "the botanists (or the zoologists) speak of *growth*, attribute it to a specific power of protoplasm for assimilation, and leave it alone as a fundamental phenomenon; but they are much concerned as to the distribution of new growth in innumerable specifically distinct forms. While the chemist, on the other hand, recognises it as a familiar phenomenon, and refers it to the same category as his other known examples of autocatalysis."

Later on, Brailsford Robertson upheld the autocatalytic theory with skill and learning*; and knowing well that growth was no simple solitary chemical reaction, he thought that behind it lay some one master-reaction, essentially autocatalytic, by which protoplasmic synthesis was effected or controlled. He adduced at least one curious case, in the growth and multiplication of the Infusoria, which can hardly be described otherwise than as catalytic. Two minute individuals (of *Enchelys* or *Colpodium*) kept in the same drop of water, so enhance each other's rate of asexual reproduction that it may be many times as great when two are together as when one is alone; the phenomenon has been called *allelocatalysis*. When a single infusorian is isolated, it multiplies the quicker the smaller the drop it is in—a further proof or indication that something is being given off, in this instance by the living cells, which hastens growth and reproduction. But even the ordinary multiplication of a bacterium, which doubles its numbers every few minutes till (were it not for limiting factors) those numbers would be all but incalculable in a day, looks like and has been cited as a simple but most striking instance of the potentialities of protoplasmic catalysis.

It is not necessary for us to pursue this subject much further.

* T. B. Robertson, *The Chemical Basis of Growth and Senescence*, 1923; and earlier papers. Cf. his Multiplication of isolated infusoria, *Biochem. Journ.* xv, pp. 598–611, 1921; cf. *Journ. Physiol.* LVI, pp. 404–412, 1921; R. A. Peters, Substances needed for the growth of... *Colpodium*, *Journ. Physiol.* LV, p. 1, 1921.

It is sufficiently obvious that the normal S-shaped curve of growth of an organism resembles in its general features the velocity-curve of chemical autocatalysis, and many writers have enlarged on the resemblance; but the S-shaped curve of growth of a population resembles it just as well. When the same curve depicts the growth of an individual, and of a population, and the velocity of a chemical reaction, it is enough to shew that the analogy between these is a mathematical and not a physico-chemical one. The sigmoid curve of growth, common to them all, is sufficiently explained as an interference effect, due to opposing factors such as we may use a differential equation to express: a phase of acceleration is followed by a phase of retardation, and the causes of both are in each case complex, uncertain or unknown. Nor are points of difference lacking between the chemical and the biological phenomena. As the chemical reaction draws to a close, it is by the gradual attainment of chemical equilibrium; but when organic growth comes to an end, it is (in all but the lowest organisms) by reason of a very different kind of equilibrium, due in the main to the gradual differentiation of the organism into parts, among whose peculiar properties or functions that of growth or multiplication falls into abeyance.

The analogy between organic growth and chemical autocatalysis is close enough to let us use, or try to use, just such mathematics as the chemist applies to his reactions, and so to reduce certain curves of growth to logarithmic formulae. This has been done by many, and with no little success *in simple cases*. So have we done, partially, in the case of yeast; so the statisticians and actuaries do with human populations; so we may do again, borrowing (for illustration) a certain well-known study of the growing sunflower (Figs. 79, 80). Taking our mathematics from elementary physical chemistry, we learn that:

The velocity of a reaction depends on the concentration a of the substance acted on: V varies as a ,

$$V = Ka.$$

The concentration continually decreases, so that at time t (in a monomolecular reaction),

$$V = \frac{dx}{dt} = k(a - x).$$

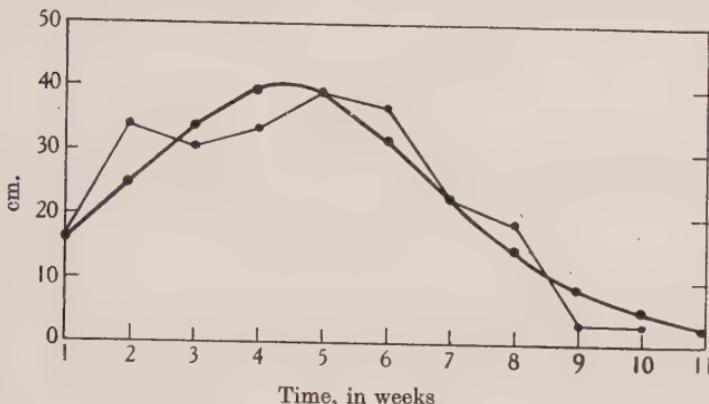


Fig. 79. Growth of sunflower-stem: observed and calculated curves.
From Reed and Holland.

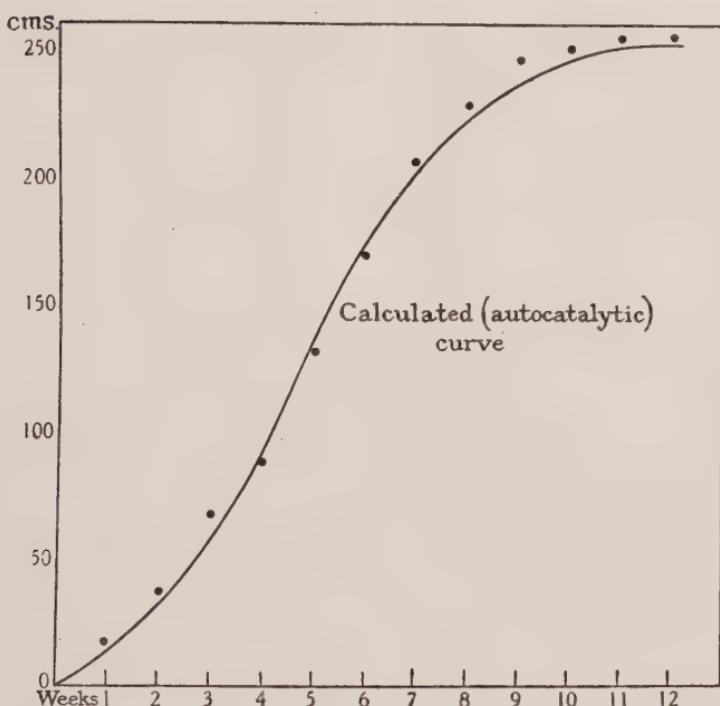


Fig. 80. Growth of sunflower-stem: calculated (autocatalytic) curve.
After Reed and Holland.

But if the substance produced exercise a catalytic effect, then the velocity will vary not only as above but will also increase as x increases: the equation becomes

$$V = \frac{dx}{dt} = k'x(a - x),$$

which is the elementary equation of autocatalysis. Integrating,

$$\frac{1}{at} \log \frac{ax}{a - x} = k'.$$

In our growth-problem it is sometimes found convenient to choose for our epoch, t' , the time when growth is half-completed, as the chemist takes the time at which his reaction is half-way through; and we may then write (with a changed constant)

$$\log \frac{x}{a - x} = K(t - t').$$

This is the physico-chemical formula which Reed and Holland apply to the growing sunflower-stem—a simple case*. For a we take the maximum height attained, viz. 254.5 cm.; for t' , the epoch when one-half of that height was reached, viz. (by interpolation) about 34.2 days. Taking an observation at random, say that for the 56th day, when the stem was 228.3 cm. high, we have

$$\log \frac{228.3}{254.5 - 228.3} = K(56 - 34.2).$$

K in this case is found to be 0.043, and the mean of all such determinations† is not far different.

Applying this formula to successive epochs, we get a calculated curve in close agreement with the observed one; and by well-known statistical methods we confirm, and measure, its "closeness of fit." But just as the chemist must vary and develop his fundamental formula to suit the course of more and more complicated reactions, so the biologist finds that only the simplest of his curves

* H. S. Reed and R. H. Holland, The growth-rate of an annual plant, *Helianthus*, *Proc. Nat. Acad. of Sci.* (Washington), v, p. 135, 1919; cf. Lotka, *op. cit.*, p. 74, A similar case is that of a gourd, recorded by A. P. Anderson, *Bull. Survey, Minnesota*, 1895, and analysed by T. B. Robertson, *ibid.* pp. 72-75.

† Better determined, especially in more complex cases, by the method of least squares.

of growth, or only portions of the rest, can be fitted to this simplest of formulae. In a life-time are many ages; and no all-embracing formula covers the infant in the womb, the suckling child, the growing schoolboy, the old man when his work is done. Besides, we need such a formula as a biologist can understand! One which gives a mere coincidence of numbers may be of little use or none, unless it go some way to depict and explain the *modus operandi* of growth. As d'Ancona puts it: "Il importe d'appliquer des formules qui correspondent non seulement au point de vue géométrique, mais soient représentées par des valeurs de signification biologique." A mere curve-diagram is better than an *empirical* formula; for it gives us at least a picture of the phenomenon, and a qualitative answer to the problem.

Growth of sunflower-stem. (After Reed and Holland)

Age (days)	Height (cm.)		1st diff.
	Observed	Calculated	
7	17.9	21.9	
14	34.4	37.7	15.8
21	67.8	62.1	24.4
28	98.1	95.4	33.3
35	131.0	134.6	39.2
42	169.0	173.0	38.4
49	205.5	204.6	31.6
56	228.3	227.2	22.6
63	247.1	241.6	14.4
70	250.5	250.1	8.5
77	253.8	255.0	4.9
84	254.5	257.8	2.8

The chemical aspect of growth

As soon as we touch on such matters as the chemical phenomenon of catalysis we are on the threshold of a subject which, if we were able to pursue it, would lead us far into the special domain of physiology; and there it would be necessary to follow it if we were dealing with growth as a phenomenon in itself, instead of mainly as a help to our study and comprehension of form. The whole question of diet, of overfeeding and underfeeding*, would present

* For example, A. S. Parker has shewn that mice suckled by rats, and consequently much overfed, grow so quickly that in three weeks they reach double their normal weight; but their development is not accelerated; *Ann. Appl. Biol.* xvi, 1929.

itself for discussion*. But without opening up this large subject, we may say one more passing word on the remarkable fact that certain chemical substances, or certain physiological secretions, have the power of accelerating or of retarding or in some way regulating growth, and of so influencing the morphological features of the organism.

To begin with there are numerous elements, such as boron, manganese, cobalt, arsenic, which serve to stimulate growth, or whose complete absence impairs or hampers it; just as there are a few others, such as selenium, whose presence in the minutest quantity is injurious or pernicious. The chemistry of the living body is more complex than we were wont to suppose.

Lecithin was shewn long ago to have a remarkable power of stimulating growth in animals†, and accelerators of plant-growth, foretold by Sachs, were demonstrated by Bottomley and others‡; the several vitamins are either accelerators of growth, or are indispensable in order that it may proceed.

In the little duckweed of our ponds and ditches (*Lemna minor*) the botanists have found a plant in which growth and multiplication are reduced to very simple terms. For it multiplies by budding, grows a rootlet and two or three leaves, and buds again; it is all young tissue, it carries no dead load; while the sun shines it has no lack of nourishment, and may spread to the limits of the pond. In one of Bottomley's early experiments, duckweed was grown (1) in a "culture solution" without stint of space or food, and (2) in the same, with the addition of a little bacterised peat or "auximone." In both cases the little plant spread freely, as in the first, or Malthusian, phase of a population curve; but the peat greatly accelerated the rate, which was not slow before. Without the auximone the population doubled in nine or ten days, and with it in five or six; but in two months the one was seventy-fold the other!

The subject has grown big from small beginnings. We know certain substances, haematin being one, which stimulate the growth of bacteria, and seem to act on them as true catalysts. An obscure but complex body known as "bios" powerfully stimulates the growth of yeast; and the so-called *auxins*, a name which covers numerous bodies both nitrogenous and non-nitrogenous, serve in

* For a brief résumé of this subject see Morgan's *Experimental Zoology*, chap. XVI.

† Hatai, *Amer. Journ. Physiology*, x, p. 57, 1904; Danilewsky, *C.R.* cxxi, cxxii, 1895-96.

‡ W. B. Bottomley, *Proc. R.S.* (B), LXXXVIII, pp. 237-247, 1914, and other papers. O. Haberlandt, *Beitr. z. allgem. Botanik*, 1921.

minute doses to accelerate the growth of the higher plants*. Some of these "growth-substances" have been extracted from moulds or from bacteria, and one remarkable one, to which the name auxin is especially applied, from seedling oats. This last is no enzyme but a stable non-nitrogenous substance, which seems to act by softening the cell-wall and so facilitating the expansion of the cell. Lastly the remarkable discovery has been made that certain indol-compounds, comparatively simple bodies, act to all intents and purposes in the same way as the growth-hormones or natural auxins, and one of these "hetero-auxins," an indol-acetic acid†, is already in common and successful use to promote the growth and rooting of cuttings.

Growth of duckweed, with and without peat-auximone

Weeks	Without		With	
	Obs.	Calc.	Obs.	Calc.
0	20	20	20	20
1	30	33	38	55
2	52	54	102	153
3	77	88	326	424
4	135	155	1,100	1,173
5	211	237	3,064	3,250
6	326	390	6,723	8,980
7	550	640	19,763	2,490
8	1052	1048	69,350	68,800
Percentage increase, per week		164 %		277 %

There are kindred matters not less interesting to the morphologist. It has long been known that the pituitary body produces, in its anterior lobe, a substance by which growth is increased and regulated. This is what we now call a "hormone"—a substance produced in one organ or tissue and regulating the functions of another. In this case atrophy of the gland leaves the subject a dwarf, and its hyper-

* The older literature is summarised by Stark, *Ergebn. d. Biologie*, II, 1906; the later by N. Nielsen, *Jb. wiss. Botan.* LXXIII, 1930; by Boyson Jensen, *Die Wuchsstofftheorie*, 1935; by F. W. Went and K. V. Thimann, *Phytohormones*, New York, 1937, and by H. L. Pearse, *Plant hormones and their practical importance*, *Imp. Bureau of Horticulture*, 1939. Cf. Went, *Rec. d. Trav. Botan. Néerl.* xxv, p. 1, 1928; A. N. J. Heyn, *ibid.* xxviii, p. 113, 1931.

† Discovered by Kögl and Kostermans, *Ztschr. f. physiol. Chem.* ccxxxv, p. 201, 1934. Cf. (*int. al.*) P. W. Zimmermann and F. W. Wilcox in *Contrib. Boyce-Thompson Instit.* 1935.

trophy or over-activity goes to the making of a giant; the limb-bones of the giant grow longer, their epiphyses get thick and clumsy, and the deformity known as "acromegaly" ensues*. This has become a familiar illustration of functional regulation, by some glandular or "endocrinial" secretion, some enzyme or *harmozone* as Gley called it, or *hormone*† as Bayliss and Starling called it—in the particular case where the function to be regulated is growth, with its consequent influence on form. But we may be sure that this so-called regulation of growth is no simple and no specific thing, but implies a far-reaching and complicated influence on the bodily metabolism‡.

Some say that in large animals the pituitary is apt to be disproportionately large§; and the giant dinosaur *Brachiosaurus*, hugest of land animals, is reputed to have the largest hypophyseal recess (or cavity for the pituitary body) ever observed.

The thyroid also has its part to play in growth, as Gudernatsch was the first to shew||; perhaps it acts, as Uhlenhorth suggests, by releasing the pituitary hormone. In a curious race of dwarf frogs both thyroid and pituitary were found to be atrophied¶. When tadpoles are fed on thyroid their legs grow out long before the usual time; on the other hand removal of the thyroid delays metamorphosis, and the tadpoles remain tadpoles to an unusual size**.

The great American bull-frog (*R. Catesbeiana*) lives for two or three years in tadpole form; but a diet of thyroid turns the little tadpoles into bull-frogs before they are a month old ††. The converse

* Cf. E. A. Schafer, The function of the pituitary body, *Proc. R.S. (B)*, LXXXI, p. 442, 1904.

† It is not easy to draw a line between *enzyme* and *vitamin*, or between *hormone* and *enzyme*.

‡ The physiological relations between insulin and the pituitary body might seem to indicate that it is the carbohydrate metabolism which is more especially concerned. Cf. (e.g.) Eric Holmes, *Metabolism of the Living Tissue*, 1937.

§ Van der Horst finds this to be the case in *Zalophus* and in the ostrich, compared with smaller seals or birds; cf. Ariens Kappers, *Journ. Anat.* LXIV, p. 256, 1930.

|| Gudernatsch, in *Arch. f. Entw. Mech.* XXXV, 1912.

¶ Eidmann, *ibid.* XLIX, pp. 510–537, 1921.

** Allen, *Journ. Exp. Zool.* XXIV, p. 499, 1918. Cf. (*int. al.*) E. Uhlenhuth, Experimental production of gigantism, *Journ. Gen. Physiol.* III, p. 347; IV, p. 321, 1921–22.

†† W. W. Swingle, *Journ. Exp. Zool.* XXIV, 1918; XXXVII, 1923; *Journ. Gen. Physiol.* I, II, 1918–19; etc.

experiment has been performed on ordinary tadpoles*; with their thyroids removed they remain normal to all appearance, but the weeks go by and metamorphosis does not take place. Gill-clefts and tail persist, no limbs appear, brain and gut retain their larval features; but months after, or apparently at any time, the belated tadpoles respond to a diet of thyroid, and may be turned into frogs by means of it. The Mexican axolotl is a grown-up tadpole which, when the ponds dry up (as they seldom do), completes its growth and turns into a gill-less, lung-breathing newt or salamander†; but feed it on thyroid, even for a single meal, and its metamorphosis is hastened and ensured‡.

Much has been done since these pioneering experiments, all going to shew that the thyroid plays its active part in the tissue-changes which accompany and constitute metamorphosis. It looks as though more thyroid meant more respiratory activity, more oxygen-consumption, more oxidative metabolism, more tissue-change, hence earlier bodily development§. Pituitary and thyroid are very different things; the one enhances growth, the other retards it. Thyroid stimulates metabolism and hastens development, but the tissues waste.

It is a curious fact, but it has often been observed, that starvation or inanition has, in the long run, a similar effect of hastening metamorphosis||. The meaning of this phenomenon is unknown.

An extremely remarkable case is that of the "galls", brought into existence on various plants in response to the prick of a small insect's ovipositor. One tree, an oak for instance, may bear galls

* Bennett Allen, *Biol. Bull.* xxxii, 1917; *Journ. Exp. Zool.* xxiv, 1918; xxx, 1920; etc.

† Colorado axolotls are much more apt to metamorphose than the Mexican variety.

‡ Babak, Ueber die Beziehung der Metamorphose...zur inneren Secretion, *Centralbl f. Physiol.* x, 1913. Cf. Abderhalden, Studien über die von einzelnen Organen hervorgebrachten Substanzen mit spezifischer Wirkung, *Pflüger's Archiv*, clxii, 1915.

§ Certain experiments by M. Morse (*Journ. Biol. Chem.* xix, 1915) seemed to shew that the effect of thyroid on metamorphosis depended on iodine; but the case is by no means clear (cf. O. Shinryo, *Sci. Rep. Tohoku Univ.* iii, 1928, and others). The axolotl is said to shew little response to experimental iodine, and its ally *Necturus* none at all (cf. B. M. Allen, in *Biol. Reviews*, xiii, 1939).

|| Cf. Krizensky, Die beschleunigende Einwirkung des Hungerns auf die Metamorphose, *Biol. Centralbl.* xliv, 1914. Cf. *antea*, p. 170.

of many kinds, well-defined and widely different, each caused to grow out of the tissues of the plant by a chemical stimulus contributed by the insect, in very minute amount; and the insects are so much alike that the galls are easier to distinguish than the flies. The same insect may produce the same gall on different plants, for instance on several species of willow; or sometimes on different parts, or tissues, of the same plant. Small pieces of a dead larva have been used to infect a plant, and a gall of the usual kind has resulted. Beyerinck killed the eggs with a hot wire as soon as they were deposited in the tree, yet the galls grew as usual. Here, as Needham has lately pointed out, is a great field for reflection and future experiment. The minute drop of fluid exuded by the insect has marvellous properties. It is not only a stimulant of growth, like any ordinary auxin or hormone; it causes the growth of a peculiar tissue, and shapes it into a new and specific form*.

Among other illustrations (which are plentiful) of the subtle influence of some substance upon growth, we have, for instance, the growth of the placental decidua, which Loeb shewed to be due to a substance given off by the corpus luteum, lending to the uterine tissues an enhanced capacity for growth, to be called into action by contact with the ovum or even of a foreign body. Various sexual characters, such as the plumage, comb and spurs of the cock, arise in like manner in response to an internal secretion or "male hormone"; and when castration removes the source of the secretion, well-known morphological changes take place. When a converse change takes place the female acquires, in greater or less degree, characters which are proper to the male: as in those extreme cases, known from time immemorial, when an old and barren hen assumes the plumage of the cock†.

The mane of the lion, the antlers of the stag, the tail of the peacock, are all examples of intensified differential growth, or localised and

* Joseph Needham, Aspects nouveaux de la chimie et de la biologie de la croissance organisée, *Folia Morphologica*, Warszawa, VIII, p. 32, 1938. On galls, see (*int. al.*) Cobbold, Ross und Hedicke, *Die Pflanzengallen*, Jena, 1927; etc. And on their "morphogenic stimulus", cf. Herbst, *Biolog. Cblt.*, 1894–5, passim.

† The hen which assumed the voice and plumage of the male was a portent or omen —*gallina cecinit*. The first scientific account was John Hunter's celebrated Account of an extraordinary pheasant, and Of the appearance of the change of sex in Lady Tynte's peahen, *Phil. Trans.* LXX, pp. 527, 534, 1780.

sex-linked hypertrophy; and in the singular and striking plumage of innumerable birds we may easily see how enhanced growth of a tuft of feathers, perhaps exaggeration of a single plume, is at the root of the whole matter. Among extreme instances we may think of the immensely long first primary of the pennant-winged nightjar; of the long feather over the eye in *Pteridophora alberti*,



Fig. 81. A single pair of hypertrophied feathers in a bird-of-paradise, *Pteridophora alberti*.

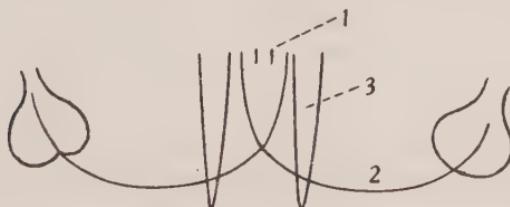


Fig. 82. Unequal growth in the three pairs of tail-feathers of a humming-bird (*Loddigesia*). 1, rudimentary; 2, short and stiff; 3, long and spathulate.

or the six long plumes over or behind the eye in the six-shafted bird-of-paradise; or among the humming-birds, of the long outer rectrix in *Lesbia*, the second outer one in *Aethusa*, or of the extraordinary inequalities of the tail-feathers of *Loddigesia mirabilis*, some rudimentary, some short and straight and stiff, and other two immensely elongated, curved and spathulate. The sexual hormones have a potent influence on the plumage of a bird; they serve, somehow, to orientate and regulate the rate of growth from one feather-tract to another, and from one end to another, even from one side to the other, of a single feather. An extreme case is the occasional pheno-

menon of a "gynandrous" feather, male and female on two sides of the same vane*.

While unequal or differential growth is of peculiar interest to the morphologist, rate of growth pure and simple, with all the agencies which control or accelerate it, remains of deeper importance to the practical man. The live-stock breeder keeps many desirable qualities in view: constitution, fertility, yield and quality of milk or wool are some of these; but rate of growth, with its corollaries of early maturity and large ultimate size, is generally more important than them all. The inheritance of size is somewhat complicated, and limited from the breeder's point of view by the mother's inability to nourish and bring forth a crossbred offspring of a breed larger than her own. A cart mare, covered by a Shetland sire, produces a good-sized foal; but the Shetland mare, crossed with a carthorse, has a foal a little bigger, but not much bigger, than herself (Fig. 83). In size and rate of growth, as in other qualities, our farm animals differ vastly from their wild progenitors, or from the "un-improved" stock in days before Bakewell and the other great breeders began. The improvement has been brought about by "selection"; but what lies behind? Endocrine secretions, especially pituitary, are doubtless at work; and already the stock-raiser and the biochemist may be found hand in hand.

If we once admit, as we are now bound to do, the existence of factors which by their physiological activity, and apart from any direct action of the nervous system, tend towards the acceleration of growth and consequent modification of form, we are led into wide fields of speculation by an easy and a legitimate pathway. Professor Gley carries such speculations a long, long way: for he says† that by these chemical influences "Toute une partie de la construction des êtres paraît s'expliquer d'une façon toute mécanique. La forteresse, si longtemps inaccessible, du vitalisme est entamée. Car la notion morphogénique était, suivant le mot de Dastre‡, comme 'le dernier réduit de la force vitale'."

* See an interesting paper by Frank R. Lillie and Mary Juhn, on The physiology of development of feathers: I, Growth-rate and pattern in the individual feather. *Physiological Zoology*, v. pp. 124-184, 1932, and many papers quoted therein.

† Le Néo-vitalisme, *Revue Scientifique*, March 1911.

‡ *La Vie et la Mort*, 1902, p. 43.

The physiological speculations we need not discuss: but, to take a single example from morphology, we begin to understand the possibility, and to comprehend the probable meaning, of the all but sudden appearance on the earth of such exaggerated and almost monstrous forms as those of the great secondary reptiles and the

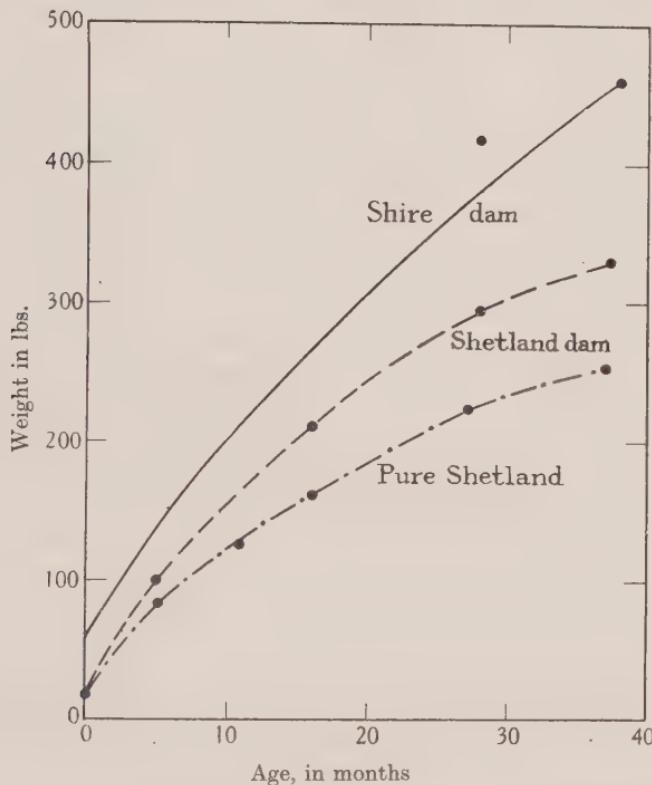


Fig. 83. Effect of cross-breeding on rate of growth in Shetland ponies.
From Walton and Hammond's data.*

great tertiary mammals†. We begin to see that it is in order to account not for the appearance but for the disappearance of such forms as these that natural selection must be invoked. And we then, I think, draw near to the conclusion that what is true of these is universally true, and that the great function of natural selection

* Walton and Hammond, *Proc. R.S. (B)*, No. 840, p. 317, 1938.

† Cf. also Dendy, *Evolutionary Biology*, 1912, p. 408.

is not to originate* but to remove: *donec ad interitum genus id natura redegit†*:

The world of things living, like the world of things inanimate, grows of itself, and pursues its ceaseless course of creative evolution. It has room, wide but not unbounded, for variety of living form and structure, as these tend towards their seemingly endless but yet strictly limited possibilities of permutation and degree: it has room for the great and for the small, room for the weak and for the strong. Environment and circumstance do not always make a prison, wherein perforce the organism must either live or die; for the ways of life may be changed, and many a refuge found, before the sentence of unfitness is pronounced and the penalty of extermination paid. But there comes a time when "variation," in form, dimensions, or other qualities of the organism, goes further than is compatible with all the means at hand of health and welfare for the individual and the stock; when, under the active and creative stimulus of forces from within and from without, the active and creative energies of growth pass the bounds of physical and physiological equilibrium: and so reach the limits which, as again Lucretius tells us, natural law has set between what may and what may not be,

et quid quaeque queant per foedera naturai
quid porro nequeant.

Then, at last, we are entitled to use the customary metaphor, and to see in natural selection an inexorable force whose function is not to create but to destroy—to weed, to prune, to cut down and to cast into the fire‡.

* So said Yves Delage (*L'hérédité*, 1903, p. 397): "La sélection naturelle est un principe admirable et parfaitement juste. Tout le monde est d'accord sur ce point. Mais où l'on n'est pas d'accord, c'est sur la limite de sa puissance et sur la question de savoir si elle peut engendrer des formes spécifiques nouvelles. *Il semble bien démontré aujourd'hui qu'elle ne le peut pas.*"

† Lucret. v, 875. "Lucretius nowhere seems to recognise the possibility of improvement or change of species by 'natural selection'; the animals remain as they were at the first, except that the weaker and more useless kinds have been crushed out. Hence he stands in marked contrast with modern evolutionists." Kelsey's note, *ad loc.*

‡ Even after we have so narrowed its scope and sphere, natural selection is still a hard saying; for the causes of extinction are wellnigh as hard to understand as are those of the origin of species. If we assert (as has been lightly and too

Of regeneration, or growth and repair

The phenomenon of regeneration, or the restoration of lost or amputated parts, is a particular case of growth which deserves separate consideration. It is a property manifested in a high degree among invertebrates and many cold-blooded vertebrates, diminishing as we ascend the scale, until it lessens down in the warm-blooded animals to that *vis medicatrix* which heals a wound. Ever since the days of Aristotle, and still more since the experiments of Trembley, Réaumur and Spallanzani in the eighteenth century, physiologist and psychologist alike have recognised that the phenomenon is both perplexing and important. "Its discovery," said Spallanzani, "was an immense addition to the riches of organic philosophy, and an inexhaustible source of meditation for the philosopher." The general phenomenon is amply treated of elsewhere*, and we need only deal with it in its immediate relation to growth.

Regeneration, like growth in other cases, proceeds with a velocity which varies according to a definite law; the rate varies with the time, and we may study it as velocity and as acceleration. Let us take, as an instance, Miss M. L. Durbin's measurements of the rate of regeneration of tadpoles' tails: the rate being measured in terms of length, or longitudinal increment†. From a number of tadpoles, whose average length was in one experiment 34 mm., and in another 49 mm., about half the tail was cut off, and the average amounts regenerated in successive periods are shewn as follows:

Days	3	5	7	10	12	14	17	18	24	28	30
Amount regenerated (mm.):											
First experiment	1.4	—	3.4	4.3	—	5.2	—	5.5	6.2	—	6.5
Second „	0.9	2.2	3.7	5.2	6.0	6.4	7.1	—	7.6	8.2	8.4

confidently done) that Smilodon perished on account of its gigantic tusks, that Teleosaurus was handicapped by its exaggerated snout, or Stegosaurus weighed down by its intolerable load of armour, we may call to mind kindred forms where similar conditions did not lead to rapid extermination, or where extinction ensued apart from any such apparent and visible disadvantages. Cf. F. A. Lucas, *On momentum in variation*, *Amer. Nat.* xli, p. 46, 1907.

* See Professor T. H. Morgan's *Regeneration* (316 pp.), 1901, for a full account and copious bibliography. The early experiments on regeneration, by Vallisneri, Dicquemare, Spallanzani, Réaumur, Trembley, Baster, Bonnet and others, are epitomised by Haller, *Elementa Physiologiae*, viii, pp. 156 seq.

† *Journ. Exper. Zool.* vii, p. 397, 1909.

Both experiments give us fairly smooth curves of growth within the period of the observations; and, with a slight and easy extrapolation, both curves draw to the base-line at zero (Fig. 84). More-

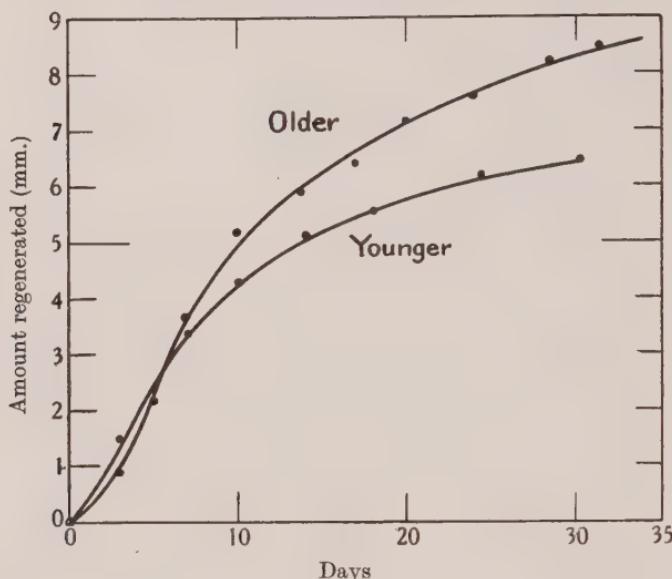


Fig. 84. Curve of regenerative growth in tadpoles' tails.
From M. L. Durbin's data.

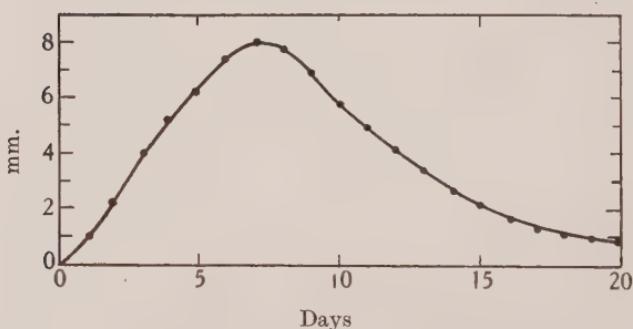


Fig. 85. Tadpoles' tails: amount regenerated daily, in mm.
(Smoothed curve).

over, if from the smoothed curves we deduce the daily increments, we get (Fig. 85) a bell-shaped curve similar to (or to all appearance identical with) a skew curve of error. In point of fact, this instance of regeneration is a very ordinary example of *growth*, with its

S-shaped curve of integration and its bell-shaped differential curve, just as we have seen it in simple cases, or simple phases, of the growth of a population or an individual.

If we amputate one limb of a pair in some animal with rapid powers of regeneration, we may compare from time to time the dimensions of the regenerating limb with those of its uninjured fellow, and so deal with a relative rather than an absolute velocity. The legs of insect-larvae are easily restored, but after pupation no further growth or regeneration takes place. An easy experiment, then, is to remove a limb in larvae of various ages, and to compare

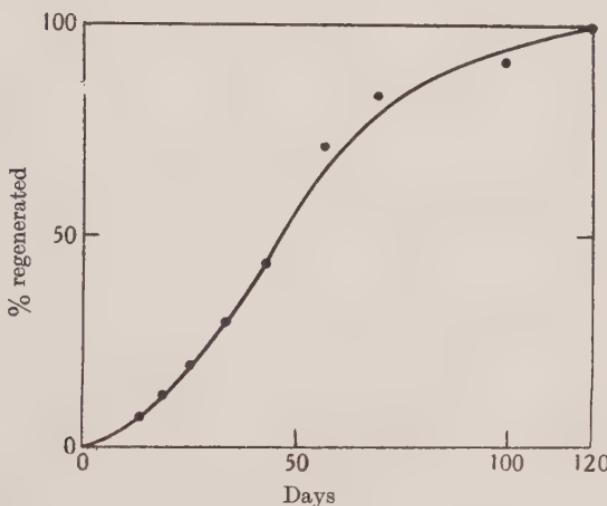


Fig. 86. Regenerative growth in mealworms' legs.

at leisure in the pupa the dimensions of the new limb with the old. The following much-abbreviated table shews the gradual increase of a regenerating limb in a mealworm, up to final equality with the normal limb, the rate varying according to the usual S-shaped curve* (Fig. 86).

*Rate of regeneration in the mealworm (*Tenebrio molitor, larva*)*

Days after amputation	...	0	16	21	25	34	44	58	70	100	121
% ratio of new limb to old		0	7	11	20	29	42	71	83	91	100

* From J. Krizenecky, Versuch zur statisch-graphischen Untersuchung... der Regenerationsvorgänge, *Arch. f. Entw. Mech.* xxxix, 1914; xlii, 1917.

Some writers have found the curve of regenerative growth to be different from the curve of ordinary growth, and have commented on the apparent difference; but they have been misled (as it seems to me) by the fact that regeneration is seen from the start or very nearly so, while the ordinary curves of growth, as they are usually presented to us, date not from the beginning of growth, but from the comparatively late, and unimportant, and even fallacious epoch of birth. A complete curve of growth, starting from zero, has the same essential characteristics as the regeneration curve.

Indeed the more we consider the phenomenon of regeneration, the more plainly does it shew itself to us as but a particular case of the general phenomenon of growth*, following the same lines, obeying the same laws, and merely started into activity by the special stimulus, direct or indirect, caused by the infliction of a wound. Neither more nor less than in other problems of physiology are we called upon, in the case of regeneration, to indulge in metaphysical speculation, or to dwell upon the beneficent purpose which seemingly underlies this process of healing and repair.

It is a very general rule, though not a universal one, that regeneration tends to fall somewhat short of a *complete* restoration of the lost part; a certain percentage only of the lost tissues is restored. This fact was well known to some of those old investigators, who, like the Abbé Trembley and like Voltaire, found a fascination in the study of artificial injury and the regeneration which followed it. Sir John Graham Dalyell, for instance, says, in the course of an admirable paragraph on regeneration†: "The reproductive faculty...is not confined to one portion, but may extend over many; and it may ensue even in relation to the regenerated portion more than once. Nevertheless, the faculty gradually weakens, so that in general every successive regeneration is smaller and more imperfect than the organisation preceding it; and at length it is exhausted."

* The experiments of Loeb on the growth of *Tubularia* in various saline solutions, referred to on p. 245, might as well or better have been referred to under the heading of regeneration, as they were performed on cut pieces of the zoophyte. (Cf. Morgan, *op. cit.* p. 35.)

† *Powers of the Creator*, I, p. 7, 1851. See also *Rare and Remarkable Animals*, II, pp. 17-19, 90, 1847.

In certain minute animals, such as the Infusoria, in which the capacity for regeneration is so great that the entire animal may be restored from a mere fragment, it becomes of great interest to discover whether there be some definite size at which the fragment ceases to display this power. This question has been studied by Lillie*, who found that in *Stentor*, while still smaller fragments were capable of surviving for days, the smallest portions capable of regeneration were of a size equal to a sphere of about 80μ in diameter, that is to say of a volume equal to about one twenty-seventh of the average entire animal. He arrives at the remarkable conclusion that for this, and for all other species of animals, there is a "minimal organisation mass," that is to say a "minimal mass of definite size consisting of nucleus and cytoplasm within which the organisation of the species can just find its latent expression." And in like manner, Boveri† has shewn that the fragment of a sea-urchin's egg capable of growing up into a new embryo, and so discharging the complete functions of an entire and uninjured ovum, reaches its limit at about one-twentieth of the original egg—other writers having found a limit at about one-fourth. These magnitudes, small as they are, represent objects easily visible under a low power of the microscope, and so stand in a very different category to the minimal magnitudes in which life itself can be manifested, and which we have discussed in another chapter.

The Bermuda "life-plant" (*Bryophyllum calycinum*) has so remarkable a power of regeneration that a single leaf, kept damp, sprouts into fresh leaves and rootlets which only need nourishment to grow into a new plant. If a stem bearing two opposite leaves be split asunder, the two co-equal sister-leaves will produce (as we might indeed expect) *equal masses* of shoots in equal times, whether these shoots be many or few; and, if one leaf of the pair have part cut off it and the other be left intact, the amount of new growth

* F. R. Lillie, The smallest parts of *Stentor* capable of regeneration, *Journ. Morphology*, XII, p. 239, 1897.

† Boveri, Entwicklungsfähigkeit kernloser Seeigeleier, etc., *Arch. f. Entw. Mech.* II, 1895. See also Morgan, Studies of the partial larvae of *Sphaerechinus*, *ibid.* 1895; J. Loeb, On the limits of divisibility of living matter, *Biol. Lectures*, 1894; *Pflüger's Archiv*, LIX, 1894, etc. Bonnet studied the same problem a hundred and seventy years ago, and found that the smallest part of the worm *Lumbriculus* capable of regenerating was $1\frac{1}{2}$ lines (3·4 mm.) long. For other references and discussion see H. Przibram, *Form und Formel*, 1922, ch. v.

will be in direct and precise proportion to the mass of the leaf from which it grew. The leaf is all the while a living tissue, manufacturing material to build its own offshoots; and we have a simple case of the law of mass action in the relation between the mass of the leaf with its included chlorophyll and that of its regenerated offshoot*.

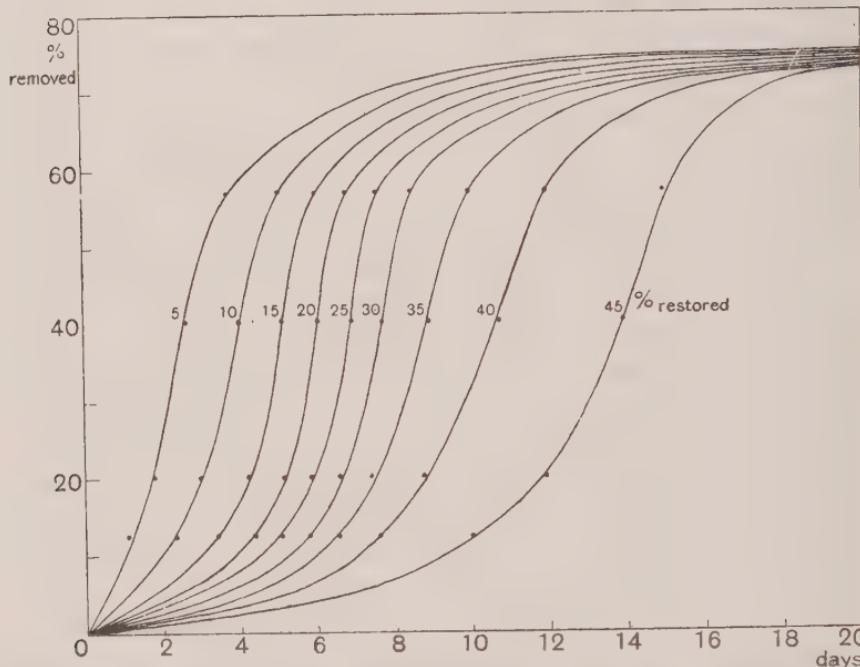


Fig. 87. Relation between the percentage amount of tail removed, the percentage restored, and the time required for its restoration. Constructed from M. M. Ellis's data.

A number of phenomena connected with the linear rate of regeneration are illustrated and epitomised in the accompanying diagram (Fig. 87), which I have constructed from certain data given by Ellis in a paper on the relation of the amount of tail regenerated to the amount removed, in tadpoles. These data are summarised in the next table. The tadpoles were all very much

* Jacques Loeb, The law controlling the quantity and rate of regeneration, *Proc. Nat. Acad. Sci.* iv, pp. 117-121, 1918; *Journ. Gen. Physiol.* 1, pp. 81-96, 1918; *Botan. Gaz.* LXV, pp. 150-174, 1918.

of a size, about 40 mm.; the average length of tail was very near to 26 mm., or 65 per cent. of the whole body-length; and in four series of experiments about 10, 20, 40 and 60 per cent. of the tail were severally removed. The amount regenerated in successive intervals of three days is shewn in our table. By plotting the actual amounts regenerated against these three-day intervals of time, we may interpolate values for the time taken to regenerate definite percentage amounts, 5 per cent., 10 per cent., etc. of the amount removed; and my diagram is constructed from the four sets of values thus obtained, that is to say from the four sets of experiments which differed from one another in the amount of tail amputated. To these we have to add the general result of a fifth series of experiments, which shewed that when as much as 75 per cent. of the tail was cut off, no regeneration took place at all, but the animal presently died. In our diagram, then, each curve indicates the time taken to regenerate n per cent. of the amount removed. All the curves converge towards infinity of time, when the amount removed approaches 75 per cent. of the whole; and all start from zero, for nothing is regenerated where nothing had been destroyed.

The rate of regenerative growth in tadpoles' tails

(After M. M. Ellis, *Journ. Exp. Zool.* vii, p. 421, 1909)

Series*	Body length mm.	Tail length mm.	Amount removed mm.	Per cent. removed	% amount regenerated in days						
					3	6	9	12	15	18	32
O	39.575	25.895	3.2	12.36	13	31	44	44	44	44	44
P	40.21	26.13	5.28	20.20	10	29	40	44	44	44	44
R	39.86	25.70	10.4	40.50	6	20	31	40	48	48	48
S	40.34	26.11	14.8	56.7	0	16	33	39	45	48	48

* Each series gives the mean of 20 experiments.

The amount regenerated varies also with the age of the tadpole, and with other factors such as temperature; in short, for any given age or size of tadpole, and for various temperatures, and doubtless for other varying physical conditions, a similar diagram might be constructed †.

The power of reproducing, or regenerating, a lost limb is par-

† Cf. also C. Zeleny, Factors controlling the rate of regeneration, *Illinois Biol. Monographs*, III, p. 1, 1916.

ticularly well developed in arthropod animals, and is sometimes accompanied by remarkable modification of the form of the regenerated limb. A case in point, which has attracted much attention, occurs in connection with the claws of certain Crustacea*.

In many of these we have an asymmetry of the great claws, one being larger than the other and also more or less different in form. For instance in the common lobster, one claw, the larger of the two, is provided with a few great "crushing" teeth, while the smaller claw has more numerous teeth, small and serrated. Though Aristotle thought otherwise, it appears that the crushing-claw may be on the right or left side, indifferently; whether it be on one or the other is a matter of "chance." It is otherwise in many other Crustacea, where the larger and more powerful claw is always left or right, as the case may be, according to the species: where, in other words, the "probability" of the large or the small claw being left or being right is tantamount to certainty†.

As we have already seen, the one claw is the larger because it has grown the faster; it has a higher "coefficient of growth," and accordingly, as age advances, the disproportion between the two claws becomes more and more evident. Moreover, we must assume that the characteristic form of the claw is a "function" of its magnitude; the knobbiness is a phenomenon coincident with growth, and we never, under any circumstances, find the smaller claw with big crushing teeth and the big claw with little serrate ones. There are many other somewhat similar cases where size and form are manifestly correlated, and we have already seen, to some extent, how the phenomenon of growth is often accompanied by such ratios of velocity as lead inevitably to changes of form. Meanwhile, then, we must simply assume that the essential difference between the two claws is one of magnitude, with which a certain differentiation of form is inseparably associated.

* Cf. H. Przibram, Scheerenumkehr bei dekapoden Crustaceen, *Arch. f. Entw. Mech.* xix, pp. 181-247, 1905; xxv. pp. 266-344, 1907; Emmel, *ibid.* xxii, p. 542, 1906; Regeneration of lost parts in lobster, *Rep. Comm. Inland Fisheries, Rhode Island*, xxxv., xxxvi., 1905-6; *Science* (N.S.), xxvi., pp. 83-87, 1907; Zeleny, Compensatory regulation, *Journ. Exp. Zool.* II, pp. 1-102, 347-369, 1905; etc.

† Lobsters are occasionally found with two symmetrical claws: which are then usually serrated, sometimes (but very rarely) both blunt-toothed. Cf. W. T. Calman, *P.Z.S.* 1906, pp. 633, 634, and *reff.*

If we amputate a claw, or if, as often happens, the crab "casts it off," it undergoes a process of regeneration—it grows anew, and does so with an accelerated velocity which ceases when equilibrium of the parts is once more attained: the accelerated velocity being a case in point to illustrate that *vis revulsionis* of Haller to which we have already referred.

With the help of this principle, Przibram accounts for certain curious phenomena which accompany the process of regeneration. As his experiments and those of Morgan shew, if the large or knobby claw (*A*) be removed, there are certain cases, e.g. the common lobster, where it is directly regenerated. In other cases, e.g. *Alpheus**[†], the other claw (*B*) assumes the size and form of that which was amputated, while the latter regenerates itself in the form of the lesser and weaker one; *A* and *B* have apparently changed places. In a third case, as in the hermit-crabs, the *A*-claw regenerates itself as a small or *B*-claw, but the *B*-claw remains for a time unaltered, though slowly and in the course of repeated moults it later on assumes the large and heavily toothed *A*-form.

Much has been written on this phenomenon, but in essence it is very simple. It depends upon the respective rates of growth, upon a ratio between the rate of regeneration and the rate of growth of the uninjured limb: that is to say, on the familiar phenomenon of unequal growth, or, as it has been called, *heterogony**. It is complicated a little, however, by the possibility of the uninjured limb growing all the faster for a time after the animal has been relieved of the other. From the time of amputation, say of *A*, *A* begins to grow from zero, with a high "regenerative" velocity; while *B*, starting from a definite magnitude, continues to increase with its normal or perhaps somewhat accelerated velocity. The ratio between the two velocities of growth will determine whether, by a given time, *A* has equalled, outstripped, or still fallen short of the magnitude of *B*.

That this is the gist of the whole problem is confirmed (if confirmation be necessary) by certain experiments of Wilson's. It is

* E. B. Wilson, Reversal of symmetry in *Alpheus heterochelus*, *Biol. Bull.* iv, p. 197, 1903.

† See p. 205.

known that by section of the nerve to a crab's claw, its growth is retarded, and as the general growth of the animal proceeds the claw comes to appear stunted or dwarfed. Now in such a case as that of *Alpheus*, we have seen that the rate of regenerative growth in an amputated large claw fails to let it reach or overtake the magnitude of the growing little claw: which latter, in short, now appears as the big one. But if at the same time as we amputate the big claw we also sever the nerve to the lesser one, we so far slow down the latter's growth that the other is able to make up to it, and in this case the two claws continue to grow at approximately equal rates, or in other words continue of coequal size.

The phenomenon of regeneration goes some little way towards helping us to comprehend the phenomenon of "multiplication by fission," as it is exemplified in its simpler cases in many worms and worm-like animals. For physical reasons which we shall have to study in another chapter, there is a natural tendency for any tube, if it have the properties of a fluid or semi-fluid substance, to break up into segments after it comes to a certain length*; and nothing can prevent its doing so except the presence of some controlling force, such for instance as may be due to the pressure of some external support, or some superficial thickening or other intrinsic rigidity of its own substance. If we add to this natural tendency towards fission of a cylindrical or tubular worm, the ordinary phenomenon of regeneration, we have all that is essentially implied in "reproduction by fission." And in so far as the process rests upon a physical principle, or natural tendency, we may account for its occurrence in a great variety of animals, zoologically dissimilar; and for its presence here and absence there, in forms which are materially different in a physical sense, though zoologically speaking they are very closely allied.

But the phenomena of regeneration, like all the other phenomena of growth, soon carry us far afield, and we must draw this long discussion to a close.

* A morphological *polarity*, or essential difference between one end and the other of a segment, is important even in so simple a case as the internode of a hydroid zoophyte; and an electrical polarity seems always to accompany it. Cf. A. P. Matthews, *Amer. Journ. Physiology*, VIII, p. 294, 1903; E. J. Lund, *Journ. Exper. Zool.* XXXIV, pp. 477-493; XXXVI, pp. 477-494, 1921-22.

Summary and Conclusion

For the main features which appear to be common to all curves of growth we may hope to have, some day, a simple explanation. In particular we should like to know the plain meaning of that point of inflection, or abrupt change from an increasing to a decreasing velocity of growth, which all our curves, and especially our acceleration curves, demonstrate the existence of, provided only that they include the initial stages of the whole phenomenon: just as we should also like to have a full physical or physiological explanation of the gradually diminishing velocity of growth which follows, and which (though subject to temporary interruption or abeyance) is on the whole characteristic of growth in all cases whatsoever. In short, the characteristic form of the curve of growth in length (or any other linear dimension) is a phenomenon which we are at present little able to explain, but which presents us with a definite and attractive problem for future solution. It would look as though the abrupt change in velocity must be due, either to a change in that pressure outwards from within by which the "forces of growth" make themselves manifest, or to a change in the resistances against which they act, that is to say the *tension* of the surface; and this latter force we do not by any means limit to "surface-tension" proper, but may extend to the development of a more or less resistant membrane or "skin," or even to the resistance of fibres or other histological elements binding the boundary layers to the parts within*. I take it that the sudden arrest of velocity is much more likely to be due to a sudden increase of resistance than to a sudden diminution of internal energies: in other words, I suspect that it is coincident with some notable event of histological differentiation, such as the rapid formation of a comparatively firm skin; and that the dwindling of velocities, or the negative acceleration, which follows, is the resultant or composite effect of waning forces of growth on the one hand, and increasing superficial resistance

* It is natural to suppose the cell-wall less rigid, or more plastic, in the growing tissue than in the full-grown or resting cell. It has been suggested that this plasticity is due to, or is increased by, auxins, whether in the course of nature, or in our stimulation of growth by the use of these bodies. Cf. H. Söding, *Jahrb. d. wiss. Bot.* LXXIV, p. 127, 1931.

on the other. This is as much as to say that growth, while its own energy tends to increase, leads also, after a while, to the establishment of resistances which check its own further increase.

Our knowledge of the whole complex phenomenon of growth is so scanty that it may seem rash to advance even this tentative suggestion. But yet there are one or two known facts which seem to bear upon the question, and to indicate at least the manner in which a varying resistance to expansion may affect the velocity of growth. For instance, it has been shewn by Frazee* that electrical stimulation of tadpoles, with small current density and low voltage, increases the rate of regenerative growth. As just such an electrification would tend to lower the surface-tension, and accordingly decrease the external resistance, the experiment would seem to support, in some slight degree, the suggestion which I have made.

To another important aspect of regeneration we can do no more than allude. The Planarian worms rival *Hydra* itself in their powers of regeneration; and in both cases even small bits of the animal are likely to include endoderm cells capable of intracellular digestion, whereby the fragment is enabled to live and to grow. Now if a Planarian worm be cut in separate pieces and these be suffered to grow and regenerate, they do so in a definite and orderly way; that part of a slice or fragment which had been nearer to the original head will develop a head, and a tail will be regenerated at the opposite end of the same fragment, the end which had been tailward in the beginning; the amputated fragments possess sides and ends, a front end and a hind end, like the entire worm; in short, they *retain their polarity*. This remarkable discovery is due to Child, who has amplified and extended it in various instructive ways. The existence of two poles, positive and negative, implies a "gradient" between them. It means that one part leads and another follows; that one part is dominant, or prepotent over the rest, whether in regenerative growth or embryonic development.

We may summarise, as follows, the main results of the foregoing discussion:

- (1) Except in certain minute organisms, whose form (like that

* *Journ. Exper. Zool.* vii, p. 457, 1909.

of a drop of water) is due to the direct action of the molecular forces, we may look upon the form of an organism as a "function of growth," or a direct consequence of growth whose rate varies in its different directions.] In a newer language we might call the form of an organism an "event in space-time," and not merely a "configuration in space."

(2) Growth varies in rate in an orderly way, or is subject, like other physiological activities, to definite "laws." The rates differ in degree, or form "gradients," from one point of an organism to another; the rates in different parts and in different directions tend to maintain more or less constant ratios to one another in each organism; and to the regularity and constancy of these relative rates of growth is due the fact that the form of the organism is in general regular and constant.

(3) Nevertheless, the ratio of velocities in different directions is not absolutely constant, but tends to alter in course of time, or to fluctuate in an orderly way; and to these progressive changes are due the changes of form which accompany development, and the slower changes which continue perceptibly in after life.

(4) Rate of growth depends on the age of the organism. It has a maximum somewhat early in life, after which epoch of maximum it slowly declines.

(5) Rate of growth is directly affected by temperature, and by other physical conditions: the influence of temperature being notably large in the case of cold-blooded or "poecilothermic" animals. Growth tends in these latter to be asymptotic, becoming slower but never ending with old age.

(6) It is markedly affected, in the way of acceleration or retardation, at certain physiological epochs of life, such as birth, puberty or metamorphosis.

✓ (7) Under certain circumstances, growth may be *negative*, the organism growing smaller; and such negative growth is a common accompaniment of metamorphosis, and a frequent concomitant of old age.

(8) The phenomenon of regeneration is associated with a large transitory increase in the rate of growth (or *acceleration* of growth) in the region of injury; in other respects regenerative growth is similar to ordinary growth in all its essential phenomena.

In this discussion of growth, we have left out of account a vast number of processes or phenomena in the physiological mechanism of the body, by which growth is effected and controlled. We have dealt with growth in its relation to magnitude, and to that relativity of magnitudes which constitutes form; and so we have studied it as a phenomenon which stands at the beginning of a morphological, rather than at the end of a physiological enquiry. Under these restrictions, we have treated it as far as possible, or in such fashion as our present knowledge permits, on strictly physical lines. That is to say, we rule "heredity" or any such concept out of our present account, however true, however important, however indispensable in another setting of the story, such a concept may be. In physics "on admet que l'état actuel du monde ne dépend que du passé le plus proche, sans être influencé, pour ainsi dire, par le souvenir d'un passé lointain*." This is the concept to which the differential equation gives expression; it is the step which Newton took when he left Kepler behind.

In all its aspects, and not least in its relation to form, the growth of organisms has many analogies, some close, some more remote, among inanimate things. As the waves grow when the winds strive with the other forces which govern the movements of the surface of the sea, as the heap grows when we pour corn out of a sack, as the crystal grows when from the surrounding solution the proper molecules fall into their appropriate places: so in all these cases, very much as in the organism itself, is growth accompanied by change of form, and by a development of definite shapes and contours. And in these cases (as in all other mechanical phenomena), we are led to equate our various magnitudes with time, and so to recognise that growth is essentially a question of rate, or of velocity.

The differences of form, and changes of form, which are brought about by varying rates (or "laws") of growth, are essentially the same phenomenon whether they be episodes in the life-history of the individual, or manifest themselves as the distinctive characteristics of what we call separate species of the race. From one form, or one ratio of magnitude, to another there is but one straight and direct road of transformation, be the journey taken fast or

* Cf. H. Poincaré, *La physique générale et la physique mathématique*, *Rev. gén. des Sciences*, xi, p. 1167, 1900.

slow; and if the transformation take place at all, it will in all likelihood proceed in the self-same way, whether it occur within the lifetime of an individual or during the long ancestral history of a race. No small part of what is known as Wolff's or von Baer's law, that the individual organism tends to pass through the phases characteristic of its ancestors, or that the life-history of the individual tends to recapitulate the ancestral history of its race, lies wrapped up in this simple account of the relation between growth and form.

But enough of this discussion. Let us leave for a while the subject of the growth of the organism, and attempt to study the conformation, within and without, of the individual cell.

CHAPTER IV

ON THE INTERNAL FORM AND STRUCTURE OF THE CELL

IN the early days of the cell-theory, a hundred years ago, Goodcir was wont to speak of cells as “centres of growth” or “centres of nutrition,” and to consider them as essentially “centres of force*”. He looked forward to a time when the forces connected with the cell should be particularly investigated: when, that is to say, minute anatomy should be studied in its dynamical aspect. “When this branch of enquiry,” he says, “shall have been opened up, we shall expect to have a science of organic forces, having direct relation to anatomy, the science of organic forms.” And likewise, long afterwards, Giard contemplated a science of *morphodynamique*—but still looked upon it as forming so guarded and hidden a “territoire scientifique, que la plupart des naturalistes de nos jours ne le verront que comme Moïse vit la terre promise, seulement de loin et sans pouvoir y entrer†.”

To the external forms of cells, and to the forces which produce and modify these forms, we shall pay attention in a later chapter. But there are forms and configurations of matter within the cell which also deserve to be studied with due regard to the forces, known or unknown, of whose resultant they are the visible expression.

* *Anatomical and Pathological Observations*, p. 3, 1845; *Anatomical Memoirs*, II, p. 392, 1868. This was a notable improvement on the “kleine wirkungsfähige Zentren oder Elementen” of the *Cellularpathologie*. Goodcir seems to have been seeking an analogy between the living cell and the physical atom, which Faraday, following Boscovich, had been speaking of as a *centre of force* in the very year before Goodcir published his *Observations*: see Faraday’s *Speculations concerning Electrical Conductivity and the Nature of Matter*, 1844. For Newton’s “molecules” had been turned by his successors into material points; and it was Boscovich (in 1758) who first regarded these material points as mere persistent centres of force. It was the same fertile conception of a *centre of force* which led Rutherford, later on, to the discovery of the nucleus of the atom.

† A. Giard, L’œuf et les débuts de l’évolution, *Bull. Sci. du Nord de la Fr.* VIII, pp. 252–258, 1876.

In the long interval since Goodsir's day, the visible structure, the conformation and configuration, of the cell, has been studied far more abundantly than the purely dynamic problems which are associated therewith. The overwhelming progress of microscopic observation has multiplied our knowledge of cellular and intracellular structure; and to the multitude of visible structures it has been often easier to attribute virtues than to ascribe intelligible functions or modes of action. But here and there nevertheless, throughout the whole literature of the subject, we find recognition of the inevitable fact that dynamical problems lie behind the morphological problems of the cell.

Bütschli pointed out sixty years ago, with emphatic clearness, the failure of morphological methods and the need for physical methods if we were to penetrate deeper into the essential nature of the cell*. And such men as Loeb and Whitman, Driesch and Roux, and not a few besides, have pursued the same train of thought and similar methods of enquiry.

Whitman†, for instance, puts the case in a nutshell when, in speaking of the so-called "caryokinetic" phenomena of nuclear division, he reminds us that the leading idea in the term "caryokinesis" is *motion*—"motion viewed as an exponent of forces residing in, or acting upon, the nucleus. It regards the nucleus as a *seat of energy, which displays itself in phenomena of motion*‡."

In short it would seem evident that, except in relation to a dynamical investigation, the mere study of cell structure has but

* *Entwickelungsvorgänge der Eizelle*, 1876; *Investigations on Microscopic Foams and Protoplasm*, p. 1, 1894.

† *Journ. Morphology*, I, p. 229, 1887.

‡ While it has been very common to look upon the phenomena of mitosis as sufficiently explained by the results *towards which* they seem to lead, we may find here and there a strong protest against this mode of interpretation. The following is a case in point: "On a tenté d'établir dans la mitose dite primitive plusieurs catégories, plusieurs types de mitose. On a choisi le plus souvent comme base de ces systèmes des concepts abstraits et télologiques: répartition plus ou moins exacte de la chromatine entre les deux noyaux-fils suivant qu'il y a ou non des chromosomes (*Dangeard*), distribution particulière et signification dualiste des substances nucléaires (substance kinétique et substance génératrice ou héréditaire, *Hartmann et ses élèves*), etc. Pour moi tous ces essais sont à rejeter catégoriquement à cause de leur caractère finaliste; de plus, ils sont construits sur des concepts non démontrés, et qui parfois représentent des généralisations absolument erronées." A. Alexeieff, *Archiv für Protistenkunde*, XIX, p. 344, 1913.

little value of its own. That a given cell, an ovum for instance, contains this or that visible substance or structure, germinal vesicle or germinal spot, chromatin or achromatin, chromosomes or centrosomes, obviously gives no explanation of the *activities* of the cell. And in all such hypotheses as that of "pangenesis," in all the theories which attribute specific properties to micellae, chromosomes, idioplasts, ids, or other constituent particles of protoplasm or of the cell, we are apt to fall into the error of attributing to *matter* what is due to *energy* and is manifested in force: or, more strictly speaking, of attributing to material particles individually what is due to the energy of their collocation.

The tendency is a very natural one, as knowledge of structure increases, to ascribe particular virtues to the material structures themselves, and the error is one into which the disciple is likely to fall but of which we need not suspect the master-mind. The dynamical aspect of the case was in all probability kept well in view by those who, like Goodsir himself, first attacked the problem of the cell and originated our conceptions of its nature and functions*.

If we speak, as Weismann and others speak, of an "hereditary substance," a substance which is split off from the parent-body, and which hands on to the new generation the characteristics of the old, we can only justify our mode of speech by the assumption that that particular portion of matter is the essential vehicle of a particular charge or distribution of energy, in which is involved the capability of producing motion, or of doing "work." For, as Newton said, to tell us that a thing "is endowed with an occult specific quality†, by which it acts and produces manifest effects, is to tell us nothing; but to derive two or three general principles of motion‡ from

* See also (*int. al.*) R. S. Lillie's papers on the physiology of cell-division in the *Journ. Exper. Physiology*; especially No. vi, Rhythmic changes in the resistance of the dividing sea-urchin egg, *ibid.* xvi, pp. 369–402, 1916.

† Such as the *virtu dormitive* which accounts for the soporific action of opium. We are now more apt, as Le Dantec says, to substitute for this occult quality the hypothetical substance *dormitin*.

‡ This is the old philosophic axiom writ large: *Ignorato motu, ignoratur natura*; which again is but an adaptation of Aristotle's phrase, *η ἀρχὴ τῆς κινήσεως*, as equivalent to the "Efficient Cause." FitzGerald holds that "all explanation consists in a description of underlying motions" (*Scientific Writings*, 1902, p. 385); and Oliver Lodge remarked, "You can move Matter; it is the only thing you can do to it."

phenomena would be a very great step in philosophy, though the causes of those principles were not yet discovered." The *things* which we see in the cell are less important than the *actions* which we recognise in the cell; and these latter we must especially scrutinise, in the hope of discovering how far they may be attributed to the simple and well-known physical forces, and how far they be relevant or irrelevant to the phenomena which we associate with, and deem essential to, the manifestation of *life*. It may be that in this way we shall in time draw nigh to the recognition of a specific and ultimate residuum.

And lacking, as we still do lack, direct knowledge of the actual forces inherent in the cell, we may yet learn something of their distribution, if not also of their nature, from the outward and inward configuration of the cell and from the changes taking place in this configuration; that is to say from the movements of matter, the kinetic phenomena, which the forces in action set up.

The fact that the germ-cell develops into a very complex structure is no absolute proof that the cell itself is structurally a very complicated mechanism: nor yet does it prove, though this is somewhat less obvious, that the forces at work or latent within it are especially numerous and complex. If we blow into a bowl of soapsuds and raise a great mass of many-hued and variously shaped bubbles, if we explode a rocket and watch the regular and beautiful configuration of its falling streamers, if we consider the wonders of a limestone cavern which a filtering stream has filled with stalactites, we soon perceive that in all these cases we have begun with an initial system of very slight complexity, whose structure in no way foreshadowed the result, and whose comparatively simple intrinsic forces only play their part by complex interaction with the equally simple forces of the surrounding medium. In an earlier age, men sought for the visible embryo, even for the *homunculus*, within the reproductive cells; and to this day we scrutinise these cells for visible structure, unable to free ourselves from that old doctrine of "pre-formation*."

Moreover, the microscope seemed to substantiate the idea (which

* As when Nägeli concluded that the organism is, in a certain sense, "vorgebildet"; *Beitr. zur wiss. Botanik*, II, 1860.

we may trace back to Leibniz* and to Hobbes†), that there is no limit to the mechanical complexity which we may postulate in an organism, and no limit, therefore, to the hypotheses which we may rest thereon. But no microscopical examination of a stick of sealing-wax, no study of the material of which it is composed, can enlighten us as to its electrical manifestations or properties. Matter of itself has no power to do, to make, or to become: it is in energy that all these potentialities reside, energy invisibly associated with the material system, and in interaction with the energies of the surrounding universe.

That "function presupposes structure" has been declared an accepted axiom of biology. Who it was that so formulated the aphorism I do not know; but as regards the structure of the cell it harks back to Brücke, with whose demand for a mechanism, or an organisation, within the cell histologists have ever since been trying to comply‡. But unless we mean to include thereby invisible, and merely chemical or molecular, structure, we come at once on dangerous ground. For we have seen in a former chapter that organisms are known of magnitudes so nearly approaching the molecular, that everything which the morphologist is accustomed to conceive as "structure" has become physically impossible; and recent research tends to reduce, rather than to extend, our conceptions of the visible structure necessarily inherent in living protoplasm§. The microscopic structure which in the last resort

* "La matière arrangée par une sagesse divine doit être essentiellement organisée partout... il y a machine dans les parties de la machine naturelle à l'infini." *Sur le principe de la Vie*, p. 431 (Erdmann). This is the very converse of the doctrine of the Atomists, who could not conceive a condition "*ubi dimidiae partis pars semper habebit Dimidiā partem, nec res praefiniet ulla.*"

† Cf. an interesting passage from the *Elements* (I, p. 445, Molesworth's edit.), quoted by Owen, *Hunterian Lectures on the Invertebrates*, 2nd ed. pp. 40, 41, 1855.

‡ "Wir müssen deshalb den lebenden Zellen, abgesehen von der Molekular-structur der organischen Verbindungen welche sie enthält, noch eine andere und in anderer Weise complicirte Structur zuschreiben, und diese es ist welche wir mit dem Namen *Organisation* bezeichnen," Brücke, *Die Elementarorganismen*, *Wiener Sitzungsber.* XLIV, 1861, p. 386; quoted by Wilson, *The Cell*, etc., p. 289. Cf. also Hardy, *Journ. Physiol.* xxiv, 1899, p. 159.

§ The term *protoplasm* was first used by Purkinje, about 1839 or 1840 (cf. Reichert, *Arch. f. Anat. u. Physiol.* 1841). But it was better defined and more strictly used by Hugo von Mohl in his paper *Ueber die Saftbewegung im Inneren der Zellen*, *Botan. Zeitung*, IV, col. 73-78, 89-94, 1846.

or in the simplest cases it seems to shew, is that of a more or less viscous colloid, or rather mixture of colloids, and nothing more. Now, as Clerk Maxwell puts it in discussing this very problem, "one material system can differ from another only in the configuration and motion which it has at a given instant*." If we cannot assume differences in structure or configuration, we must assume differences in *motion*, that is to say in *energy*. And if we cannot do this, then indeed we are thrown back upon modes of reasoning unauthorised in physical science, and shall find ourselves constrained to assume, or to "admit, that the properties of a germ are not those of a purely material system."

But we are by no means necessarily in this dilemma. For though we come perilously near to it when we contemplate the lowest orders of magnitude to which life has been attributed, yet in the case of the ordinary cell, or ordinary egg or germ which is going to develop into a complex organism, if we have no reason to assume or to believe that it comprises an intricate "mechanism," we may be quite sure, both on direct and indirect evidence, that, like the powder in our rocket, it is very heterogeneous in its structure. It is a mixture of substances of various kinds, more or less fluid, more or less mobile, influenced in various ways by chemical, electrical, osmotic and other forces, and in their admixture separated by a multitude of surfaces or boundaries, at which these or certain of these forces are made manifest.

Indeed, such an arrangement as this is already enough to constitute a "mechanism"; for we must be very careful not to let our physical or physiological concept of mechanism be narrowed to an interpretation of the term derived from the complicated contrivances of human skill. From the physical point of view, we understand by a "mechanism" whatsoever checks or controls, and guides into determinate paths, the workings of energy: in other words, whatsoever leads in the degradation of energy to its manifestation in some form of *work*, at a stage short of that ultimate degradation which lapses in uniformly diffused heat. This, as Warburg has well explained, is the general effect or function of the physiological machine, and in particular of that part of it which we call "cell-

* Precisely as in the Lucretian *concursus, motus, ordo, positura, figurae*, whereby bodies *mutato ordine mutant naturam*.

structure*.” The normal muscle-cell is something which turns energy, derived from oxidation, into work; it is a mechanism which arrests and utilises the chemical energy of oxidation in its downward course; but the same cell when injured or disintegrated loses its “usefulness,” and sets free a greatly increased proportion of its energy in the form of heat. It was a saying of Faraday’s, that “even a life is but a chemical act prolonged. If death occur, the more rapidly oxygen and the affinities run on to their final state†.”

Very great and wonderful things are done by means of a mechanism (whether natural or artificial) of extreme simplicity. A pool of water, by virtue of its surface, is an admirable mechanism for the making of waves; with a lump of ice in it, it becomes an efficient and self-contained mechanism for the making of currents. Music itself is made of simple things—a reed, a pipe, a string. The great cosmic mechanisms are stupendous in their simplicity; and, in point of fact, every great or little aggregate of heterogeneous matter (not identical in “phase”) involves, *ipso facto*, the essentials of a mechanism. Even a non-living colloid, from its intrinsic heterogeneity, is in this sense a mechanism, and one in which energy is manifested in the movement and ceaseless rearrangement of the constituent particles. For this reason Graham speaks somewhere or other of the colloid state as “the dynamic state of matter”; in the same philosopher’s phrase, it possesses “*energia*‡.”

Let us turn then to consider, briefly and diagrammatically, the structure of the cell, a fertilised germ-cell or ovum for instance, not in any vain attempt to correlate this structure with the structure or properties of the resulting and yet distant organism; but merely to see how far, by the study of its form and its changing internal configuration, we may throw light on certain forces which are for the time being at work within it.

We may say at once that we can scarcely hope to learn more of these forces, in the first instance, than a few facts regarding their

* Otto Warburg, Beiträge zur Physiologie der Zelle, insbesondere über die Oxidationsgeschwindigkeit in Zellen; in Asher-Spiro’s *Ergebnisse der Physiologie*, xiv, pp. 253–337, 1914 (see p. 315).

† See his *Life* by Bence Jones, II, p. 299.

‡ Both phrases occur, side by side, in Graham’s classical paper on Liquid diffusion applied to analysis, *Phil. Trans.* clx, p. 184, 1861; *Chem. and Phys. Researches* (ed. Angus Smith), 1876, p. 554.

direction and magnitude; the nature and specific identity of the force or forces is a very different matter. This latter problem is likely to be difficult of elucidation, for the reason, among others, that very different forces are often much alike in their outward and visible manifestations. So it has come to pass that we have a multitude of discordant hypotheses as to the nature of the forces acting within the cell, and producing in cell division the "caryokinetic" figures of which we are about to speak. One student may, like Rhumbler, choose to account for them by an hypothesis of mechanical traction, acting on a reticular web of protoplasm*; another, like Leduc, may shew us how in many of their most striking features they may be admirably simulated by salts diffusing in a colloid medium; others, like Lamb and Graham Cannon, have compared them to the stream-lines produced and the field of force set up by bodies vibrating in a fluid; others, like Gallardo† and Rhumbler in his earlier papers‡, insisted, on their resemblance to certain phenomena of electricity and magnetism§; while Hartog believed that the force in question is only analogous to these, and has a specific identity of its own||. All these conflicting views are of secondary importance, so long as we seek only to account for certain *configurations* which reveal the direction, rather than the nature, of a force. One and the same system of lines of force may appear in a field of magnetic or of electrical energy, of the osmotic energy of diffusion, of the gravitational energy of a flowing stream. In short, we may expect to learn something of the pure or abstract dynamics long before we can deal with the special physics of the

* L. Rhumbler, Mechanische Erklärung der Aehnlichkeit zwischen magnetischen Kraftliniensystemen und Zelltheilungsfiguren, *Arch. f. Entw. Mech.* xv, p. 482, 1903.

† A. Gallardo, Essai d'interprétation des figures caryocinétiques, *Anales del Museo de Buenos-Aires* (2), II, 1896; *Arch. f. Entw. Mech.* xxviii, 1909, etc.

‡ *Arch. f. Entw. Mech.* III, IV, 1896–97.

§ On various theories of the mechanism of mitosis, see (e.g.) Wilson, *The Cell in Development*, etc.; Meves, *Zelltheilung*, in Merkel u. Bonnet's *Ergebnisse der Anatomie*, etc., VII, VIII, 1897–98; Ida H. Hyde, *Amer. Journ. Physiol.* XII, pp. 241–275, 1905; and especially A. Prenant, Théories et interprétations physiques de la mitose, *Journ. de l'Anat. et Physiol.* XLVI, pp. 511–578, 1910. See also A. Conard, *Sur le mécanisme de la division cellulaire, et sur les bases morphologiques de la Cytologie*, Bruxelles, 1939: a work which I find hard to follow.

|| M. Hartog, Une force nouvelle: le mitokinétisme, *C.R.* 11 Juli 1910; *Arch. f. Entw. Mech.* xxvii, pp. 141–145, 1909; cf. *ibid.* XL, pp. 33–64, 1914.

cell. For indeed, just as uniform expansion about a single centre, to whatsoever physical cause it may be due, will lead to the configuration of a sphere, so will any two centres or foci of potential (of whatsoever kind) lead to the configurations with which Faraday first made us familiar under the name of "lines of force*"; and this is as much as to say that the phenomenon, though physical in the concrete, is in the abstract purely mathematical, and in its very essence is neither more nor less than *a property of three-dimensional space*.

But as a matter of fact, in this instance, that is to say in trying to explain the leading phenomena of the caryokinetic division of the cell, we shall soon perceive that any explanation which is based, like Rhumbler's, on mere mechanical traction, is obviously inadequate, and we shall find ourselves limited to the hypothesis of some polarised and polarising force, such as we deal with, for instance, in magnetism or electricity, or in certain less familiar phenomena of hydrodynamics. Let us speak first of the cell itself, as it appears in a state of rest, and let us proceed afterwards to study the more active phenomena which accompany its division.

Our typical cell is a spherical body; that is to say, the uniform surface-tension at its boundary is balanced by the outward resistance of uniform forces within. But at times the surface-tension may be a fluctuating quantity, as when it produces the rhythmical contractions or "Ransom's waves"† on the surface of a trout's egg; or again, the surface-tension may be locally unequal and variable, giving rise to an amoeboid figure, as in the egg of *Hydra*‡.

Within the cell is a nucleus or germinal vesicle, also spherical,

* The configurations, as obtained by the usual experimental methods, were of course known long before Faraday's day, and constituted the "convergent and divergent magnetic curves" of eighteenth century mathematicians. As Leslie said, in 1821, they were "regarded with wonder by a certain class of dreaming philosophers, who did not hesitate to consider them as the actual traces of an invisible fluid, perpetually circulating between the poles of the magnet." Faraday's great advance was to interpret them as indications of *stress in a medium*—of tension or attraction along the lines, and of repulsion transverse to the lines, of the diagram.

† W. H. Ransom, On the ovum of osseous fishes, *Phil. Trans.* CLVII, pp. 431–502, 1867 (*vide* p. 463 *et seq.*) (Ransom, afterwards a Nottingham physician, was Huxley's friend and class-fellow at University College, and beat him for the medal in Grant's class of zoology.)

‡ Cf. also the curious phenomenon in a dividing egg described as "spinning" by Mrs G. F. Andrews, *Journ. Morph.* XII, pp. 367–389, 1897.

and consisting of portions of "chromatin," aggregated together within a more fluid drop. The fact has often been commented upon that, in cells generally, there is no correlation of *form* (though there apparently is of *size*) between the nucleus and the "cytoplasm," or main body of the cell. So Whitman* remarks that "except during the process of division the nucleus seldom departs from its typical spherical form. It divides and sub-divides, ever returning to the same round or oval form.... How different with the cell. It preserves the spherical form as rarely as the nucleus departs from it. Variation in form marks the beginning and the end of every important chapter in its history." On simple dynamical grounds, the contrast is easily explained. So long as the fluid substance of the nucleus is qualitatively different from, and incapable of mixing with, the fluid or semi-fluid protoplasm surrounding it, we shall expect it to be, as it almost always is, of spherical form. For on the one hand, it has a surface of its own whose surface-tension is presumably uniform, and on the other, it is immersed in a medium which transmits on all sides a uniform fluid or "hydrostatic" pressure†; thus the case of the spherical nucleus is closely akin to that of the spherical yolk within the bird's egg. Again, for a similar reason, the contractile vacuole of a protozoon is spherical‡. It is just a drop of fluid, bounded by a

* Whitman, *Journ. Morph.* II, p. 40, 1889.

† "Souvent il n'y a qu'une séparation *physique* entre le cytoplasme et le suc nucléaire, comme entre deux liquides immiscibles, etc."; Alexeieff, Sur la mitose dite primitive, *Arch. f. Protistenk.* XXIX, p. 357, 1913.

‡ The appearance of "vacuolation" is a result of endosmosis, or the diffusion of a less dense fluid into the denser plasma of the cell. But while water is probably taken up at the surface of the cell by purely passive osmotic intake, a definite "vacuole" appears at a place where osmotic work is being actively done. A higher osmotic pressure than that of the external medium is maintained within the cell, but as a "steady state" rather than a condition of equilibrium, in other words by the continual expenditure of energy; and the difference of pressure is at best small. The "contractile vacuole" bursts when it touches the surface of the cell, and bursting may be delayed by manipulating the vacuole towards the interior. It may sometimes burst towards the interior of the cell through inequalities in its own surface-tension, and the collapsing vacuole is then apt to shew a star-shaped figure. The cause of the higher osmotic pressure within the cell is a matter for the colloid chemist, and cannot be discussed here. On the physiology of the contractile vacuole, see (*int. al.*) H. Z. Gow, *Arch. f. Protistenk.* LXXXVII, pp. 185-212, 1936; J. Spek, Einfluss der Salze auf die Plasmkolloide von *Actinosphaerium*, *Acta Zool.* 1921; J. A. Kitching, *Journ. Exp. Biology*, XI, XIII, XV, 1934-38.

uniform surface-tension, and through whose boundary-film diffusion is taking place; but here, owing to the small difference between the fluid constituting and that surrounding the drop, the surface-tension equilibrium is somewhat unstable; it is apt to vanish, and the rounded outline of the drop disappears, like a burst bubble, in a moment.

If, on the other hand, the substance of the cell acquire a greater solidity, as for instance in a muscle-cell, or by reason of mucous accumulations in an epithelium cell, then the laws of fluid pressure no longer apply, the pressure on the nucleus tends to become unsymmetrical, and its shape is modified accordingly. Amoeboid movements may be set up in the nucleus by anything which disturbs the symmetry of its own surface-tension; and where "nuclear material" is scattered in small portions throughout the cell as in many Rhizopods, instead of being aggregated in a single nucleus, the simple explanation probably is that the "phase difference" (as the chemists say) between the nuclear and the protoplasmic substance is comparatively slight, and the surface-tension which tends to keep them separate is correspondingly small*.

Apart from that invisible or ultra-microscopic heterogeneity which is inseparable from our notion of a "colloid," there is a visible heterogeneity of structure within both the nucleus and the outer protoplasm. The former contains, for instance, a rounded nucleolus or "germinal spot," certain conspicuous granules or strands of the peculiar substance called chromatin†, and a coarse meshwork of a protoplasmic material known as "linin" or achromatin; the outer protoplasm, or cytoplasm, is generally believed to consist throughout of a sponge-work, or rather alveolar mesh-work, of more and less fluid substances; it may contain "mitochondria," appearing in tissue-cultures as small amoeboid bodies; and lastly, there are generally to be detected (in the animal, rarely in the vegetable kingdom) one or more very minute bodies, usually in the cytoplasm sometimes within the nucleus, known as the centrosome or centrosomes.

* The elongated or curved "macronucleus" of an Infusorian is to be looked upon as a single mass of chromatin, rather than as an aggregation of particles in a fluid drop, as in the case described. It has a shape of its own, in which ordinary surface-tension plays a very subordinate part.

† First so-called by W. Flemming, in his *Zellsubstanz, Kern und Zelltheilung*, 1882.

The morphologist is accustomed to speak of a "polarity" of the cell, meaning thereby a symmetry of visible structure about a particular axis. For instance, whenever we can recognise in a cell both a nucleus and a centrosome, we may consider a line drawn through the two as the morphological axis of polarity; an epithelium cell is morphologically symmetrical about a median axis passing from its free surface to its attached base. Again, by an extension of the term polarity, as is customary in dynamics, we may have a "radial" polarity, between centre and periphery; and lastly, we may have several apparently independent centres of polarity within the single cell. Only in cells of quite irregular or amoeboid form do we fail to recognise a definite and symmetrical polarity. The *morphological* polarity is accompanied by, and is but the outward expression (or part of it) of a true *dynamical* polarity, or distribution of forces; and the lines of force are, or may be, rendered visible by concatenation of particles of matter, such as come under the influence of the forces in action.

When lines of force stream inwards from the periphery towards a point in the interior of the cell, particles susceptible of attraction either crowd towards the surface of the cell or, when retarded by friction, are seen forming lines or "fibrillae" which radiate outwards from the centre. In the cells of columnar or ciliated epithelium, where the sides of the cell are symmetrically disposed to their neighbours but the free and attached surfaces are very diverse from one another in their external relations, it is these latter surfaces which constitute the opposite poles; and in accordance with the parallel lines of force so set up, we very frequently see parallel lines of granules which have ranged themselves perpendicularly to the free surface of the cell (cf. Fig. 149).

A simple manifestation of polarity may be well illustrated by the phenomenon of diffusion, where we may conceive, and may automatically reproduce, a field of force, with its poles and its visible lines of equipotential, very much as in Faraday's conception of the field of force of a magnetic system. Thus, in one of Leduc's experiments*, if we spread a layer of salt solution over a level plate of glass, and let fall into the middle of it a drop of Indian ink, or of blood, we shall find the coloured particles travelling

* *Théorie physico-chimique de la Vie*, 1910, p. 73.

outwards from the central "pole of concentration" along the lines of diffusive force, and so mapping out for us a "monopolar field" of diffusion: and if we set two such drops side by side, their lines of diffusion will oppose and repel one another. Or, instead of the uniform layer of salt solution, we may place at a little distance from one another a grain of salt and a drop of blood, representing two opposite poles: and so obtain a picture of a "bipolar field" of diffusion. In either case, we obtain results closely analogous to the morphological, but really *dynamical*, polarity of the organic cell. But in all probability, the dynamical polarity or asymmetry of the cell is a very complicated phenomenon: for the obvious reason that, in any system, one asymmetry will tend to beget another. A chemical asymmetry will induce an inequality of surface-tension, which will lead directly to a modification of form; the chemical asymmetry may in turn be due to a process of electrolysis in a polarised electrical field; and again the chemical heterogeneity may be intensified into a chemical polarity, by the tendency of certain substances to seek a locus of greater or less surface-energy. We need not attempt to grapple with a subject so complicated, and leading to so many problems which lie beyond the sphere of interest of the morphologist. But yet the morphologist, in his study of the cell, cannot quite evade these important issues; and we shall return to them again when we have dealt somewhat with the form of the cell, and have taken account of some of its simpler phenomena.

We are now ready, and in some measure prepared, to study the numerous and complex phenomena which accompany the division of the cell, for instance of the fertilised egg. But it is no easy task to epitomise the facts of the case, and none the easier that of late new methods have shewn us new things, and have cast doubt on not a little that we have been accustomed to believe.

Division of the cell is of necessity accompanied, or preceded, by a change from a radial or monopolar to a definitely bipolar symmetry. In the hitherto quiescent or apparently quiescent cell, we perceive certain movements, which correspond precisely to what must accompany and result from a polarisation of forces within: of forces which, whatever be their specific nature, are at least

capable of polarisation, and of producing consequent attraction or repulsion between charged particles. The opposing forces which are distributed in equilibrium throughout the cell become focused in two "centrosomes*," which may or may not be already visible. It generally happens that, in the egg, one of these centrosomes is near to and the other far from the "animal pole," which is both visibly and chemically different from the other, and is where the more conspicuous developmental changes will presently begin.

Between the two centrosomes, in stained preparations, a spindle-shaped figure appears (Fig. 88), whose striking resemblance to the

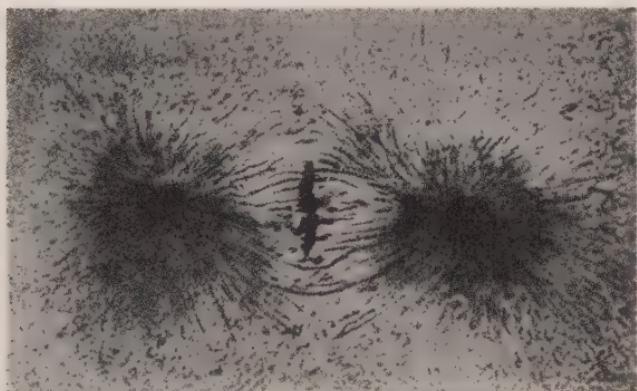


Fig. 88. Caryokinetic figure in a dividing cell (or blastomere) of a trout's egg.
After Prenant, from a preparation by Prof. Bouin.

lines of force made visible by iron-filings between the poles of a magnet was at once recognised by Hermann Fol, in 1873, when he witnessed the phenomenon for the first time†. On the farther side of the centrosomes are seen star-like figures, or "asters," in which we seem to recognise the broken lines of force which run externally to those stronger lines which lie nearer to the axis and constitute the "spindle." The lines of force are rendered visible, or materialised, just as in the experiment of the iron-filings, by the fact that, in the heterogeneous substance of the cell, certain portions

* These centrosomes are the two halves of a single granule, and are said (by Boveri) to come from the middle piece of the original spermatozoon.

† He did so in the egg of a medusa (*Geryon*), *Jen. Zeitschr.* vii, p. 476, 1873. Similar ideas have been expressed by Strasbürger, Henneguy, Van Beneden, Errera, Ziegler, Gallardo and others.

of matter are more "permeable" to the acting force than others, become themselves polarised after the fashion of a magnetic or "paramagnetic" body, arrange themselves in an orderly way between the two poles of the field of force, seem to cling to one another as it were in threads*, and are only prevented by the friction of the surrounding medium from approaching and congregating around the adjacent poles.

As the field of force strengthens, the more will the lines of force be drawn in towards the interpolar axis, and the less evident will be those remoter lines which constitute the terminal, or extrapolar, asters: a clear space, free from materialised lines of force, may thus tend to be set up on either side of the spindle, the so-called "Bütschli space" of the histologists†. On the other hand, the lines of force constituting the spindle will be less concentrated if they find a path of less resistance at the periphery of the cell: as happens in our experiment of the iron-filings, when we encircle the field of force with an iron ring. On this principle, the differences observed between cells in which the spindle is well developed and the asters small, and others in which the spindle is weak and the asters greatly developed, might easily be explained by variations in the potential of the field, the large, conspicuous asters being correlated in turn with a marked permeability of the surface of the cell.

The visible field of force, though often called the "nuclear spindle," is formed outside of, but usually near to, the nucleus.

* Whence the name "mitosis" (Greek *μίτος*, a thread), applied first by Flemming to the whole phenomenon. Kollmann (*Biol. Centralbl.* II, p. 107, 1882) called it *divisio per fila*, or *divisio laqueis implicata*. Many of the earlier students, such as Van Beneden (*Rech. sur la maturation de l'oeuf*, *Arch. de Biol.* IV, 1883), and Hermann Fol (*Zur Lehre v. d. Entstehung d. karyokinétischen Spindel*, *Arch. f. mikrosk. Anat.* XXXVII, 1891) thought they recognised actual muscular threads, drawing the nuclear material asunder towards the respective foci or poles; and some such view of *Zugkräfte* was long maintained by other writers, by Heidenhain especially, by Boveri, Flemming, R. Hertwig, Rhumbler, and many more. In fact, the existence of contractile threads, or the ascription to the spindle rather than to the poles or centrosomes of the active forces concerned in nuclear division, formed the main tenet of all those who declined to go beyond the "contractile properties of protoplasm" for an explanation of the phenomenon (cf. J. W. Jenkinson, *Q.J.M.S.* XLVIII, p. 471, 1904. See also J. Spek's historical account of the theories of cell-division, *Arch. f. Entw. Mech.* XLIV, pp. 5-29, 1918).

† Cf. O. Bütschli, *Ueber die künstliche Nachahmung der karyokineticischen Figur*, *Verh. Med. Nat. Ver. Heidelberg*, V, pp. 28-41 (1892), 1897.

Let us look a little more closely into the structure of this body, and into the changes which it presently undergoes.

Within its spherical outline (Fig. 89 A), it contains an "alveolar" meshwork (often described, from its appearance in optical section, as a "reticulum"), consisting of more solid substances with more fluid matter filling up the interalveolar spaces. This phenomenon, familiar to the colloid chemist, is what he calls a "two-phase system," one substance or "phase" forming a continuum through which the other is dispersed; it is closely allied to what we call in

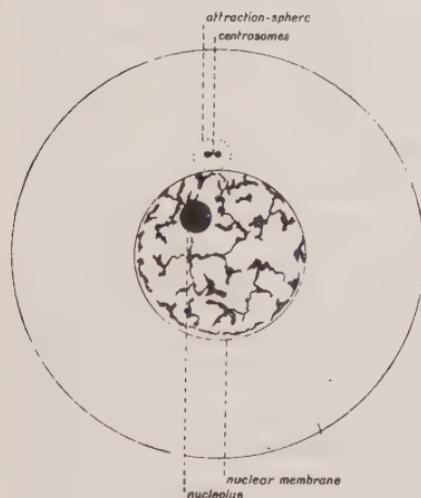


Fig. 89 A.

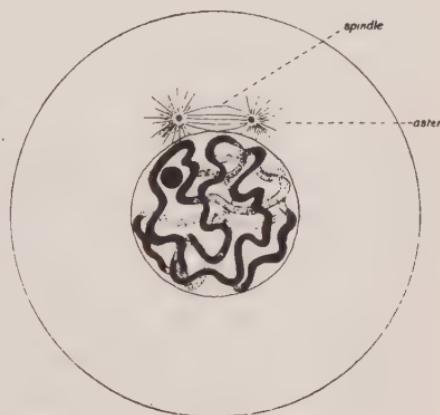


Fig. 89 B.

ordinary language a *froth* or a *foam**[†], save that in these latter the disperse phase is represented by *air*. It is a surface-tension phenomenon, due to the interaction of two intermixed fluids not very different in density, as they strive to separate. Of precisely the same kind (as Bütschli was the first to shew) are the minute alveolar networks which are to be discerned in the cytoplasm of the cell†,

* Froth and foam have been much studied of late years for technical reasons, and other factors than surface-tension are found to be concerned in their existence and their stability. See (*int. al.*) Freundlich's *Capillarchemie*, and various papers by Sasaki, in *Bull. Chem. Soc. of Japan*, 1936-39.

† Bütschli, *Untersuchungen über mikroskopische Schäume und das Protoplasma*, 1892; *Untersuchungen über Strukturen*, etc., 1898; L. Rhumbler, *Protoplasma als physikalisches System*, *Ergebn. d. Physiologie*, 1914; H. Giersberg, *Plasmabau der Amöben*, im Hinblick auf die Wabentheorie, *Arch. f. Entw. Mech.* LI, pp. 150-250, 1922; etc.

and which we now know to be not inherent in the nature of protoplasm nor of living matter in general, but to be due to various causes, natural as well as artificial*. The microscopic honeycomb structure of cast metal under various conditions of cooling is an example of similar surface-tension phenomena.

Such then, in briefest outline, is the typical structure commonly ascribed to a cell when its latent energies are about to manifest themselves in the phenomenon of cell-division. The account is based on observation not of the living cell but of the dead: on the assumption, that is to say, that fixed and stained material gives a true picture of reality. But in Robert Chambers's method of micro-dissection†, the living cell is manipulated with fine glass needles under a high magnification, and shews us many interesting things. Chambers assures us that the spindle fibres never make their appearance as visible structures until coagulation has set in; and that astral rays are, or appear to be, channels in which the more fluid content of the cell flows towards a centrosome‡. Within the bounds to which we are at present keeping, these things are of no great moment; for whether the spindle appear early or late, it still bears witness to the fact that matter has arranged itself along bipolar lines of force; and even if the astral rays be only streams or currents, on lines of force they still approximately lie. Yet the change from the old story to the new is important, and may make a world of difference when we attempt to define the forces concerned. All our descriptions, all our interpretations, are bound to be influenced by our conception of the mechanism before us; and he

* Arrhenius, in describing a typical colloid precipitate, does so in terms that are very closely applicable to the ordinary microscopic appearance of the protoplasm of the cell. The precipitate consists, he says, "en un réseau d'une substance solide contenant peu d'eau, dans les mailles duquel est inclus un fluide contenant un peu de colloïde dans beaucoup d'eau.... Évidemment cette structure se forme à cause de la petite différence de poids spécifique des deux phases, et de la consistance gluante des particules séparées, qui s'attachent en forme de réseau" (*Rev. Scientifique*, Feb. 1911). This, however, is far from being the whole story: cf. (e.g.) S. C. Bradford, On the theory of gels, *Biochem. Journ.* xvii, p. 230, 1925; W. Seifritz, The alveolar structure of protoplasm, *Protoplasma*, ix, p. 198, 1930; and A. Frey-Wissling, *Submikroskopische Morphologie des Protoplasmas*, Berlin, 1938.

† See R. Chambers, An apparatus...for the dissection and injection of living cells, *Anatom. Record*, xxiv, 19 pp., 1922.

‡ This centripetal flow of fluid was announced by Bütschli in his early papers, and confirmed by Rhumbler, though attributed to another cause.

who sees threads where another sees channels is likely to tell a different story about neighbouring and associated things.

It has also been suggested that the spindle is somehow due to a re-arrangement of protein macromolecules or micelles; that such changes of orientation of large colloid particles may be a widespread phenomenon; and that coagulation itself is but a polymerisation of larger and larger macromolecules*.

But here we have touched the brink of a subject so important that we must not pass it by without a word, and yet so contentious that we must not enter into its details. The question involved is simply whether the great mass of recorded observations and accepted beliefs with regard to the visible structure of protoplasm and of the cell constitute a fair picture of the actual *living cell*, or be based on appearances which are incident to death itself and to the artificial treatment which the microscopist is accustomed to apply. The great bulk of histological work is done by methods which involve the sudden killing of the cell or organism by strong reagents, the assumption being that death is so rapid that the visible phenomena exhibited during life are retained or "fixed" in our preparations.

Hermann Fol struck a warning note full sixty years ago: "Il importe à l'avenir de l'histologie de combattre la tendance à tirer des conclusions des images obtenues par des moyens artificiels et à leur donner une valeur intrinsèque, sans que ces images aient été contrôlées sur le vivant†." Fol was thinking especially of cell-membranes and the delimitation of cells; but still more difficult and precarious is the interpretation of the minute internal networks, granules, etc., which represent the alleged structure of protoplasm. A colloid body, or colloid solution, is *ipso facto* heterogeneous; it has after some fashion a *structure* of its own. And this structure chemical action, under the microscope, may demonstrate, or emphasise, or alter and disguise. As Hardy put it, "It is notorious that the various fixing reagents are coagulants of organic colloids, and that the figure varies according to the reagent used."

A case in point is that of the vitreous humour, to which some histologists have ascribed a fairly complex structure, seeing in it a framework of fibres with the meshes filled with fluid. But it is really a *true gel*, without any structure in the usual sense of the word. The "fibres" seen in ordinary microscopic preparations are due to the coagulation of micellae by the fixative employed. Under the ultra-microscope the vitreous is optically empty to begin with; then innumerable minute fibrillae appear in the beam of light, criss-crossing one another. Soon these break down into strings of beads, and

* Cf. J. D. Bernal, on Molecular architecture of biological systems, *Proc. Roy. Inst.*, 1938; H. Staudinger, *Nature*, Aug. 1, 1939.

† H. Fol, *Recherches sur la fécondation et le commencement de l'hénogénie chez divers animaux*, Genève, 1879, pp. 241-242. Cf. A. Dalcq, in *Biol. Reviews*, III, p. 24, 1928: "Il serait désirable de nous débarrasser de l'idée que tout ce qu'il y a d'important dans la cellule serait providentiellement colorable par l'hématoxyline, la safranine ou le violet de gentiane."

finally only separate dots are seen*. Other sources of error arise from the optical principles concerned in microscopic vision; for the diffraction-pattern which we call the "image" may, under certain circumstances, be very different from the actual object†. Furthermore, the optical properties of living protoplasm are especially complicated and imperfectly known, as in general those of colloids may be said to be; the minute aggregates of the "disperse phase" of gels produce a scattering action on light, leading to appearances of turbidity etc., with no other or more real basis‡.

So it comes to pass that some writers have altogether denied the existence in the living cell-protoplasm of a network or alveolar "foam"; others have cast doubts on the main tenets of recent histology regarding nuclear structure; and Hardy, discussing the structure of certain gland-cells, declared that "there is no evidence that the structure discoverable in the cell-substance of these cells after fixation has any counterpart in the cell when living." "A large part of it" he went on to say "is an artefact. The profound difference in the minute structure of a secretory cell of a mucous gland according to the reagent which is used to fix it would, it seems to me, almost suffice to establish this statement in the absence of other evidence§."

Nevertheless, histological study proceeds, especially on the part of the morphologists, with but little change in theory or in method, in spite of these and many other warnings. That certain visible structures, nucleus, vacuoles, "attraction-spheres" or centrosomes, etc., are actually present in the living cell we know for certain; and to this class belong the majority of structures with which we are at present concerned. That many other alleged structures are artificial has also been placed beyond a doubt; but where to draw the dividing line we often do not know.

The following is a brief epitome of the visible changes undergone by a typical cell, subsequent to the resting stage, leading up to the act of segmentation, and constituting the phenomenon of mitosis or caryokinetic division. In the fertilised egg of a sea-urchin we see with almost diagrammatic completeness, in fixed and stained specimens, what is set forth here||.

* W. S. Duke-Elder, *Journ. Physiol.* LXVIII, pp. 154–165, 1930; cf. Baermann, *Arch. f. Ophthalm.* 1923, 1926; etc.

† Abbé, *Arch. f. mikrosk. Anat.* IX, p. 413, 1874; *Gesammelte Abhandl.* I, p. 45, 1904.

‡ Cf. Rayleigh, On the light from the sky, *Phil. Mag.* (4) XLI, p. 107, 1871.

§ W. B. Hardy, On the structure of cell protoplasm, *Journ. Physiol.* XXIV, pp. 158–207, 1889; also Höber, *Physikalische Chemie der Zelle und der Gewebe*, 1902; W. Berg, Beiträge zur Theorie der Fixation, etc., *Arch. f. mikr. Anat.* LXII, pp. 367–440, 1903. Cf. (int. al.) Flemming, *Zellsubstanz, Kern und Zelltheilung*, 1882, p. 51; etc.

|| My description and diagrams (Figs. 89–93) are mostly based on those of the late Professor E. B. Wilson.

1. The chromatin, which to begin with had been dimly seen as granules on a vague achromatic reticulum (Figs. 89, 90)—perhaps no more than an histological artefact—concentrates to form a skein or *spireme*, often looked on as a continuous thread, but perhaps discontinuous or fragmented from the first. It, or its several fragments, will presently split asunder; for it is essentially double, and may even be seen as a double thread, or pair of *chromatids*, from an early stage. The *chromosomes* are portions of this double thread, which shorten down to form little rods, straight or curved, often

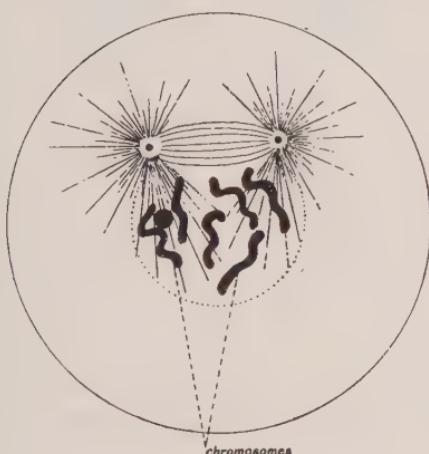


Fig. 90 A.

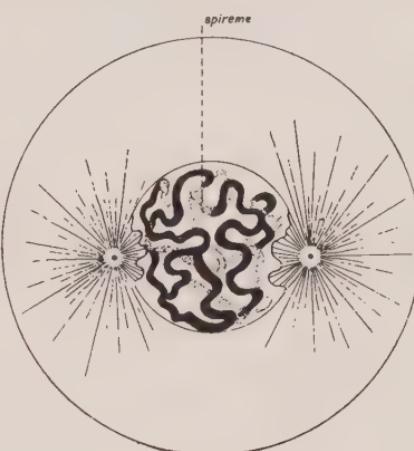


Fig. 90 B.

bent into a **V**, sometimes ovoid, round or even annular, and which in the living cell are frequently seen in active, writhing movement, “like eels in a box”*; they keep apart from one another, as by some repulsion, and tend to move outward towards the nuclear membrane. Certain deeply staining masses, the nucleoli, may be present in the resting nucleus, but take no part (at least as a rule) in the formation of the chromosomes; they are either cast out of the nucleus and dissolved in the cytoplasm, or else fade away *in situ*.

* T. S. Strangeways, *Proc. R.S. (B)*, xciv, p. 139, 1922. The tendency of the chromatin to form spirals, large or small, while the nucleus is issuing from its resting-stage, is very remarkable. The tensions to which it is due may be overcome, and the chromosomes made to uncoil, by treatment with ammonia or acetic acid vapour. See Y. Kuwada, *Botan. Mag. Tokyo*, xlvi, p. 307, 1932; and C. D. Darlington, Mechanical aspects of nuclear division, *Sci. Journ. R. Coll. of Sci.* iv, p. 94, 1934.

But this rule does not always hold; for they persist in many protozoa, and now and then the nucleolus remains and becomes itself a chromosome, as in the spermogonia of certain insects.

2. Meanwhile a certain deeply staining granule (here extra-nuclear), known as the *centrosome**, has divided into two. It is all but universally visible, save in the higher plants; perhaps less stress is laid on it than at one time, but Bovery called it the "dynamic centre" of the cell†. The two resulting granules travel to opposite poles of the nucleus, and there each becomes surrounded by a starlike figure, the *aster*, of which we have spoken already; immediately around the centrosome is a clear space, the *centrosphere*. Between the two centrosomes, or the two asters, stretches the *spindle*. It lies in the long axis, if there be one, of the cell, a rule laid down nearly sixty years ago, and still remembered as "Hertwig's Law"‡; but the rule is as much and no more than to say that the spindle sets in the direction of least resistance. Where the egg is laden with food-yolk, as often happens, the latter is heavier than the cytoplasm; and gravity, by orienting the egg itself, thus influences, though only indirectly, the first planes of segmentation§.

3. The definite nuclear outline is soon lost; for the chemical "phase-difference" between nucleus and cytoplasm has broken down, and where the nucleus was, the chromosomes now lie (Figs. 90, 91). The lines of the spindle become visible, the chromosomes arrange themselves midway between its poles, to form the *equatorial plate*, and are spaced out evenly around the central spindle, again a simple result of mutual repulsion.

4. Each chromosome separates longitudinally into two||: usually at this stage—but it is to be noted that the splitting may have taken place as early as the spireme stage (Fig. 92).

* The centrosome has a curious history of its own, none too well ascertained. The ovum has a centrosome, and in self-fertilised eggs this is retained; but when a sperm-cell enters the egg the original centrosome degenerates, and its place is taken by the "middle-piece" of the spermatozoon.

† The stages 1, 2, 5 and 6 are called by embryologists the *prophase*, *metaphase*, *anaphase* and *telophase*.

‡ C. Hertwig, *Jenaische Ztschr.* XVIII, 1884.

§ See James Gray, The effect of gravity on the eggs of *Echinus*, *Jl. Exp. Zool.* v, pp. 102–11, 1927.

|| A fundamental fact, first seen by Flemming in 1880.

5. The halves of the split chromosomes now separate from and apparently repel one another, travelling in opposite directions towards the two poles* (Fig. 92 B), for all the world as though they were being pulled asunder by actual threads.

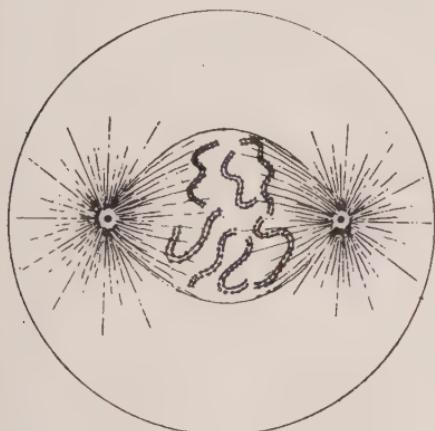


Fig. 91 A.

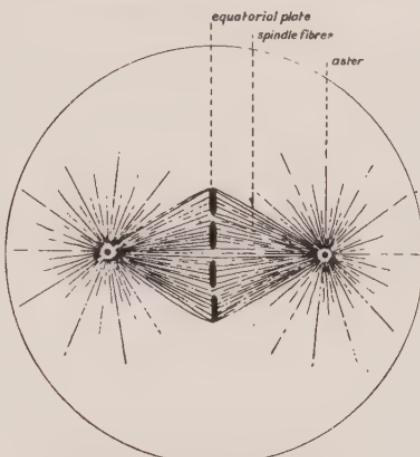


Fig. 91 B.

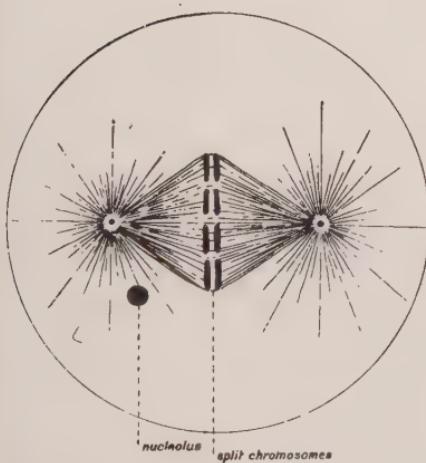


Fig. 92 A.

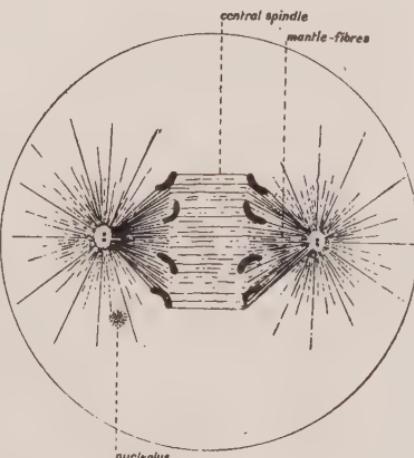


Fig. 92 B.

6. Presently the spindle itself changes shape, lengthens and contracts, and seems as it were to push the two groups of daughter-

* Cf. K. Belar, Beiträge zur Causalanalyse der Mitose, *Ztschr. f. Zellforschung*, x, pp. 73-124, 1929.

chromosomes into their new places* (Figs. 92, 93); and its chromosomes form once more an alveolar reticulum and may occasionally form another spireme at this stage. A boundary-surface, or at least a recognisable phase-difference, now develops round each reconstructed nuclear mass, and the spindle disappears (Fig. 93 B). The centrosome remains, as a rule, outside the nucleus.

7. On the central spindle, in the position of the equatorial plate, a "cell-plate," consisting of deeply staining thickenings, has made its appearance during the migration of the chromosomes. This cell-plate is more conspicuous in plant-cells.

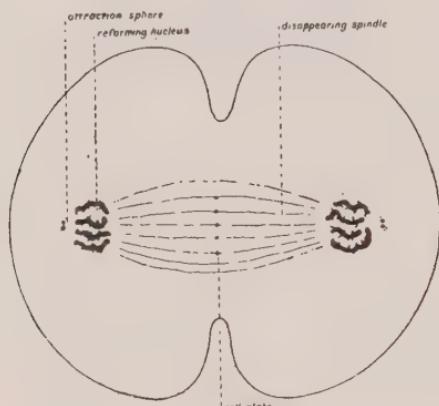


Fig. 93 A.

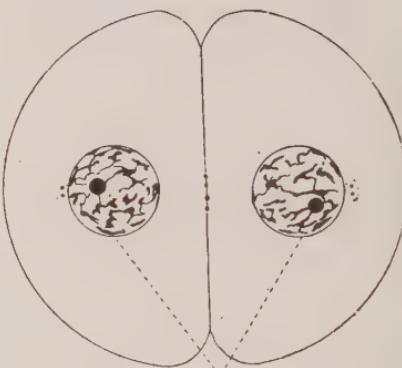


Fig. 93 B.

8. Meanwhile a constriction has appeared in the cytoplasm, and the cell divides through the equatorial plane. In plant-cells the line of this division is foreshadowed by the "cell-plate," which extends from the spindle across the entire cell, and splits into two layers, between which appears the membrane by which the daughter-cells are cleft asunder. In animal cells the cell-plate does not attain such dimensions, and no cell-wall is formed.

The whole process takes from half-an-hour to an hour; and this extreme slowness is not the least remarkable part of the phenomenon, from a physical point of view. The two halves of the

* The spindle has no actual threads or fibres, for Robert Chambers's micro-needles pass freely through it without disturbing the chromosomes: nor is it visible at all in living cells *in vitro*. It seems to be due to partial gelation of the cytoplasm, under conditions which, whether they be mechanical or chemical, are not easy to understand.

dividing centrosome, while moving apart, take some twenty minutes to travel a distance of 20μ , or at the rate, say, of two years to a yard. It is a question of inertia, and the inertia of the system must be very large.

The beautiful technique of cell-culture *in vitro* has of late years let this whole succession of phenomena, once only to be deduced from sections, be easily followed as it proceeds within the living tissue or cell. The vivid accounts which have been given of this spectacle add little to the older account as we have related it: save that, when the equatorial constriction begins and the halves of the split chromosomes drift apart, the protoplasm begins to show a curious and even violent activity. The cytoplasm is thrust in and out in bulging pustules or "balloons"; and the granules and fat-globules stream in and out as the pustules rise and fall away. At length the turmoil dies down; and now each half of the cell (not an ovum but a tissue-cell or "fibroblast") pushes out large pseudopodia, flattens into an amoeboid phase, the connecting thread of protoplasm snaps in the divided cell, and the daughter-cells fall apart and crawl away. The two groups of chromosomes, on reaching the poles of the spindle, turn into bunches of short thick rods; these grow diffuse, and form a network of chromatin within a nucleus; and at last the chromosomes, having lost their identity, disappear entirely, and two or more nucleoli are all that is to be seen within the cell.

The whole, or very nearly the whole, of these nuclear phenomena may be brought into relation with some such polarisation of forces in the cell as a whole as is indicated by the "spindle" and "asters" of which we have already spoken: certain particular phenomena, directly attributable to surface-tension and diffusion, taking place in more or less obvious and inevitable dependence upon the polar system. At the same time, in attempting to explain the phenomena, we cannot say too clearly, or too often, that all that we are meanwhile justified in doing is to try to shew that such and such actions lie *within the range* of known physical actions and phenomena, or that known physical phenomena produce effects similar to them. We feel that the whole phenomenon is not *sui generis*, but is somehow or other capable of being referred to dynamical laws, and to

the general principles of physical science. But when we speak of some particular force or mode of action, using it as an illustrative hypothesis, we stop far short of the implication that this or that force is necessarily the very one which is actually at work within the living cell; and certainly we need not attempt the formidable task of trying to reconcile, or to choose between, the various hypotheses which have already been enunciated, or the several assumptions on which they depend.

Many other things happen within the cell, especially in the germ-cell both before and after fertilisation. They also have a physical element, or a mechanical aspect, like the phenomena of cell-division which we are speaking of; but the narrow bounds to which we are keeping hold difficulties enough*.

Any region of space within which action is manifested is a field of force; and a simple example is a bipolar field, in which the action is symmetrical with reference to the line joining two points, or poles, and with reference also to the "equatorial" plane equidistant from both. We have such a field of force in the neighbourhood of the centrosome of the ripe cell or ovum, when it is about to divide; and by the time the centrosome has divided, the field is definitely a bipolar one.

The *quality* of a medium filling the field of force may be uniform, or it may vary from point to point. In particular, it may depend upon the magnitude of the field; and the quality of one medium may differ from that of another. Such variation of quality, within one medium, or from one medium to another, is capable of diagrammatic representation by a variation of the direction or the strength of the field (other conditions being the same) from the state manifested in some uniform medium taken as a standard. The medium is said to be *permeable* to the force, in greater or less degree than the standard medium, according as the variation of the density of the lines of force from the standard case, under otherwise identical conditions, is in excess or defect. *A body placed in the medium will tend to move towards regions of greater or less force according as its*

* Cf. C. D. Darlington, *Recent Advances in Cytology*, 1932, and other well-known works.

*permeability is greater or less than that of the surrounding medium**. In the common experiment of placing iron-filings between the two poles of a magnetic field, the filings have a very high permeability; and not only do they themselves become polarised so as to attract one another, but they tend to be attracted from the weaker to the stronger parts of the field, and as we have seen, they would soon gather together around the nearest pole were it not for friction or some other resistance. But if we repeat the same experiment with such a metal as bismuth, which is very little permeable to the magnetic force, then the conditions are reversed, and the particles, being repelled from the stronger to the weaker parts of the field, tend to take up their position as far from the poles as possible. The particles have become polarised, but in a sense opposite to that of the surrounding, or adjacent, field.

Now, in the field of force whose opposite poles are marked by the centrosomes, we may imagine the nucleus to act as a more or less permeable body, as a body more permeable than the surrounding medium, that is to say the "cytoplasm" of the cell. It is accordingly attracted by, and drawn into, the field of force, and tries, as it were, to set itself between the poles and as far as possible from both of them. In other words, the centrosome-foci will be apparently drawn over its surface, until the nucleus as a whole is involved within the field of force which is visibly marked out by the "spindle" (Fig. 90 B).

If the field of force be electrical, or act in a fashion analogous to an electrical field, the charged nucleus will have its surface-tensions diminished†: with the double result that the inner alveolar meshwork will be broken up (par. 1), and that the spherical boundary of the whole nucleus will disappear (par. 2). The break-up of the alveoli (by thinning and rupture of their partition walls)

* If the word *permeability* be deemed too directly suggestive of the phenomena of magnetism, we may replace it by the more general term of *specific inductive capacity*. This would cover the particular case, which is by no means an improbable one, of our phenomena being due to a "surface charge" borne by the nucleus itself and also by the chromosomes: this surface charge being in turn the result of a difference in inductive capacity between the body or particle and its surrounding medium.

† On the effect of electrical influences in altering the surface-tensions of the colloid particles, see Bredig, *Anorganische Fermente*, pp. 15, 16, 1901.

leads to the formation of a net, and the further break-up of the net may lead to the unravelling of a thread or “spireme”.

Here there comes into play a fundamental principle which, in so far as we require to understand it, can be explained in simple words. The effect (and we might even say the *object*) of drawing the more permeable body in between the poles is to obtain an “easier path” by which the lines of force may travel; but it is obvious that a longer route through the more permeable body may at length be found less advantageous than a shorter route through the less permeable medium. That is to say, the more permeable body will only tend to be drawn into the field of force until a point is reached where (so to speak) the way *round* and the way *through* are equally advantageous. We should accordingly expect that (on our hypothesis) there would be found cases in which the nucleus was wholly, and others in which it was only partially, and in greater or less degree, drawn in to the field between the centrosomes. This is precisely what is found to occur in actual fact. Figs. 90 A and B represent two so-called “types,” of a phase which follows that represented in Fig. 89. According to the usual descriptions we are told that, in such a case as Fig. 90 B, the “primary spindle” disappears* and the centrosomes diverge to opposite poles of the nucleus; such a condition being found in many plant-cells, and in the cleavage-stages of many eggs. In Fig. 90 A, on the other hand, the primary spindle persists, and subsequently comes to form the main or “central” spindle; while at the same time we see the fading away of the nuclear membrane, the breaking up of the spireme into separate chromosomes, and an ingrowth into the nuclear area of the “astral rays”—all as in Fig. 91 A, which represents the next succeeding phase of Fig. 90 B. This condition, of Fig. 91 A, occurs in a variety of cases; it is well seen in the epidermal cells of the salamander, and is also on the whole characteristic of the mode of formation of the “polar bodies†.” It is clear and obvious that the two “types” correspond to mere differences of degree,

* The spindle is potentially there, even though (as Chambers assures us) it only becomes visible after post-mortem coagulation. It is also said to become visible under crossed nicols: W. J. Schmidt, *Biodynamica*, xxii, 1936.

† These were first observed in the egg of a pond-snail (*Limnaea*) by B. Dumortier, *Mém. sur l'embryogénie des mollusques*, Bruxelles, 1837.

and are such as would naturally be brought about by differences in the relative permeabilities of the nuclear mass and of the surrounding cytoplasm, or even by differences in the magnitude of the former body.

But now an important change takes place, or rather an important difference appears; for, whereas the nucleus as a whole tended to be drawn in to the *stronger* parts of the field, when it comes to break up we find, on the contrary, that its contained spireme-thread or separate chromosomes tend to be repelled to the *weaker* parts. Whatever this difference may be due to—whether, for instance, to actual differences of permeability, or possibly to differences in “surface-charge” or to other causes—the fact is that the chromatin substance now *behaves* after the fashion of a “diamagnetic” body, and is repelled from the stronger to the weaker parts of the field. In other words, its particles, lying in the inter-polar field, tend to travel towards the equatorial plane thereof (Figs. 91, 92), and further tend to move outwards towards the periphery of that plane, towards what the histologist calls the “mantle-fibres,” or outermost of the lines of force of which the spindle is made up (par. 5, Fig. 91 b). And if this comparatively non-permeable chromatin substance come to consist of separate portions, more or less elongated in form, these portions, or separate “chromosomes,” will adjust themselves longitudinally, in a peripheral equatorial circle (Figs. 92 a, b). This is precisely what actually takes place. Moreover, before the breaking up of the nucleus, long before the chromatin material has broken up into separate chromosomes, and at the very time when it is being fashioned into a “spireme,” this body already lies in a polar field, and must already have a tendency to set itself in the equatorial plane thereof. But the long, continuous spireme thread is unable, so long as the nucleus retains its spherical boundary wall, to adjust itself in a simple equatorial annulus; in striving to do so, it must tend to coil and “kink” itself, and in so doing (if all this be so), it must tend to assume the characteristic convolutions of the “spireme.”

After the spireme has broken up into separate chromosomes, these bodies come to rest in the equatorial plane, somewhere near its periphery; and here they tend to set themselves in a symmetrical arrangement (Fig. 94), such as makes for still better equilibrium.

The particles may be rounded or linear, straight or bent, sometimes annular; they may be all alike, or one or more may differ from the rest. Lying as they do in a semi-fluid medium, and subject (doubtless) to some symmetrical play of forces, it is not to be wondered at that they arrange themselves in a symmetrical configuration; and the field of force seems simple enough to let us predict, to some extent, the symmetries open to them. We do not know, we cannot safely surmise, the nature of the forces involved. In discussing Brauer's observations on the splitting of the chromatic filament, and on the symmetrical arrangement of the separate granules, in *Ascaris megalocephala*, Lillie* remarks: "This behaviour



Fig. 94. Chromosomes, undergoing splitting and separation.
After Hatschek and Flemming, diagrammatised.

is strongly suggestive of the division of a colloidal particle under the influence of its surface electrical charge, and of the effects of mutual repulsion in keeping the products of division apart." It is probable that surface-tensions between the particles and the surrounding protoplasm would bring about an identical result, and would sufficiently account for the obvious, and at first sight very curious symmetry. If we float a couple of matches in water, we know that they tend to approach one another till they lie close together, side by side; and if we lay upon a smooth wet plate four matches, half broken across, a similar attraction brings the four matches together in the form of a symmetrical cross. Whether one of these, or yet another, be the explanation of the phenomenon,

* R. S. Lillie, Conditions determining the disposition of the chromatic filaments, etc., in mitosis; *Biol. Bulletin*, viii, 1905.

it is at least plain that by some physical cause, some mutual attraction or common repulsion of the particles, we must seek to account for the symmetry of the so-called "tetrads," and other more or less familiar configurations. The remarkable annular chromosomes, shewn in Fig. 95, can be closely imitated by loops of thread upon a soapy film, when the film within the annulus is broken or its tension reduced; the balance of forces is here a simple one, between the uniform capillary tension which tends to widen out the ring and the uniform cohesion of its particles which keeps it together.

We may find other cases, at once simpler and more varied, where the chromosomes are bodies of rounded form and more or less



Fig. 95. Annular chromosomes, formed in the spermatogenesis of the mole-cricket. From Wilson, after Vom Rath.

uniform size. These also find their way to an equatorial plate; we gather (and Lamb assures us) that they are repelled from the centrosomes. They may go near the equatorial periphery, but they are not driven there; and we infer that some bond of mutual attraction holds them together. If they be free to move in a fluid medium, subject both to some common repulsion and some mutual attraction, then their circumstances are much like those of Mayer's well-known experiment of the floating magnets. A number of magnetised needles stuck in corks, all with like poles upwards, are set afloat in a basin; they repel one another, and scatter away to the sides. But bring a strong magnet (of unlike pole) overhead, and the little magnets gather in under its common attraction, while still keeping asunder through their own mutual repulsion. The symmetry of forces leads to a symmetrical configuration, which is

the mathematical expression of a physical equilibrium—and is the not too remote counterpart of the arrangement of the electrons in an atom. Be that as it may, it is found that a group of three, four or five little magnets arrange themselves at the corners of an equilateral triangle, square or pentagon; but a sixth passes within the ring, and comes to rest in the centre of symmetry of the pentagon. If there be seven magnets, six form the ring, and the seventh occupies the centre; if there be ten, there is a ring of eight and two within it; and so on, as follows*:

Number of magnets	5	6	7	8	9	10	11	12	13	14	15	16
Do. in outer ring	5	5	6	7	8	8	8	9	10	10	10	11
Do. in inner ring	0	1	1	1	1	2	3	3	3	4	5	5

When we choose from the published figures cases where the chromosomes are as nearly as possible alike in size and form—the condition necessary for our parallel to hold—then, as Lillie predicted and as Doncaster and Graham Cannon have shewn, their congruent arrangement agrees, even to a surprising degree, with what we are led to expect by theory and analogy (Fig. 96).

The break-up of the nucleus, already referred to and ascribed to a diminution of its surface-tension, is accompanied by certain diffusion phenomena which are sometimes visible to the eye; and we are reminded of Lord Kelvin's view that diffusion is implicitly associated with surface-tension changes, of which the first step is a minute puckering of the surface-skin, a sort of interdigitation with the surrounding medium. For instance, Schewiakoff has observed in *Euglypha*† that, just before the break-up of the nucleus, a system of rays appears, concentrated about it, but having nothing to do with the polar asters: and during the existence of this striation the nucleus enlarges very considerably, evidently by imbibition of fluid from the surrounding protoplasm. In short, diffusion is at work, hand in hand with, and as it were in opposition to, the surface-tensions which define the nucleus. By diffusion, hand in hand with surface-tension, the alveoli of the nuclear meshwork are formed, enlarged and finally ruptured: diffusion sets up the movements

* H. Graham Cannon, On the nature of the centrosomal force, *Journ. Genetics*, XIII, p. 55, 1923.

† Schewiakoff, Ueber die karyokinetische Kerntheilung der *Euglypha alveolata*, *Morph. Jahrb.* XIII, pp. 193–258, 1888 (see p. 216).

which give rise to the appearance of rays, or striae, around the nucleus: and through increasing diffusion and weakening surface-tension the rounded outline of the nucleus finally disappears.

As we study these manifold phenomena in the individual cases of particular plants and animals, we recognise a close identity of type coupled with almost endless variation of specific detail; and

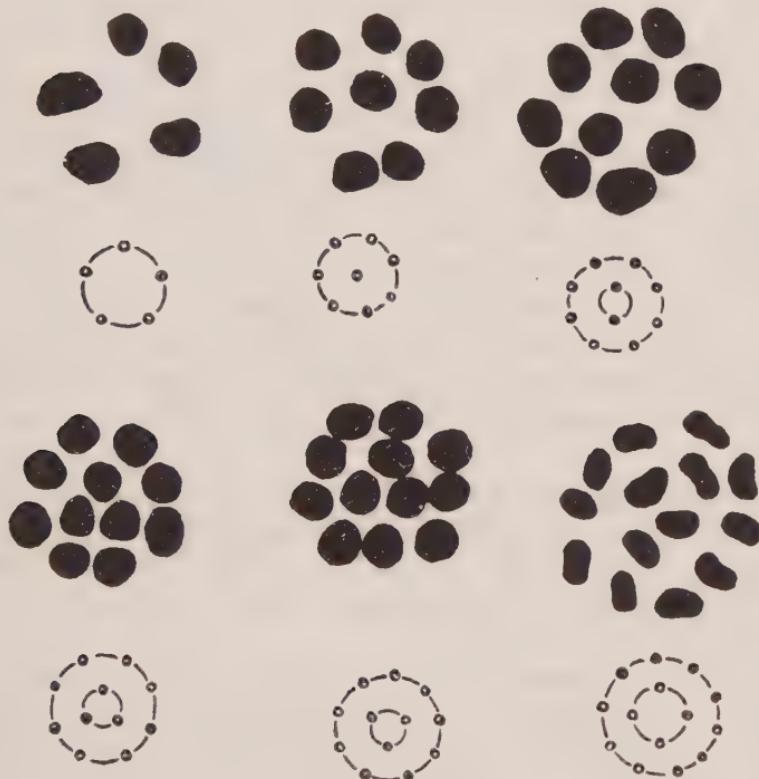


Fig. 96. Various numbers of chromosomes in the equatorial plate: the ring-diagrams give the arrangements predicted by theory. From Graham Cannon.

in particular, the order of succession in which certain of the phenomena occur is variable and irregular. The precise order of the phenomena, the time of longitudinal and of transverse fission of the chromatin thread, of the break-up of the nuclear wall, and so forth, will depend upon various minor contingencies and "interferences." And it is worthy of particular note that these variations in the order of events and in other subordinate details, while

doubtless attributable to specific physical conditions, would seem to be without any obvious classificatory meaning or other biological significance.

So far as we have now gone, there is no great difficulty in pointing to simple and familiar examples of a field of force which are similar, or comparable, to the phenomena which we witness within the cell. But among these latter phenomena there are others for which it is not so easy to suggest, in accordance with known laws, a simple mode of physical causation. It is not at once obvious how, in any system of symmetrical forces, the chromosomes, which had at first been apparently repelled from the poles towards the equatorial plane, should then be split asunder, and should presently be attracted in opposite directions, some to one pole and some to the other. Remembering that it is not our purpose to *assert* that some one particular mode of action is at work, but merely to shew that there do exist physical forces, or distributions of force, which are capable of producing the required result, I give the following suggestive hypothesis, which I owe to my colleague Professor W. Peddie.

As we have begun by supposing that the nuclear or chromosomal matter differs in *permeability* from the medium, that is to say the cytoplasm, in which it lies, let us now make the further assumption that its permeability is variable, and depends upon the *strength of the field*.

In Fig. 97, we have a field of force (representing our cell), consisting of a homogeneous medium, and including two opposite poles: lines of force are indicated by full lines, and *loci of constant magnitude of force* are shewn by dotted lines, these latter being what are known as Cayley's equipotential curves*.

Let us now consider a body whose permeability (μ) depends on the strength of the field F . At two field-strengths, such as F_a , F_b , let the permeability of the body be equal to that of the medium, and let the curved line in Fig. 98 represent generally its permeability at other field-strengths; and let the outer and inner dotted curves in Fig. 97 represent respectively the loci of the field-strengths F_b

* *Phil. Trans.* XIV, p. 142, 1857. Cf. also F. G. Teixeira, *Traité des Courbes*, I, p. 372, Coimbra, 1908.

and F_a . The body if it be placed in the medium within either branch of the inner curve, or outside the outer curve, will tend to move into the neighbourhood of the adjacent pole. If it be placed

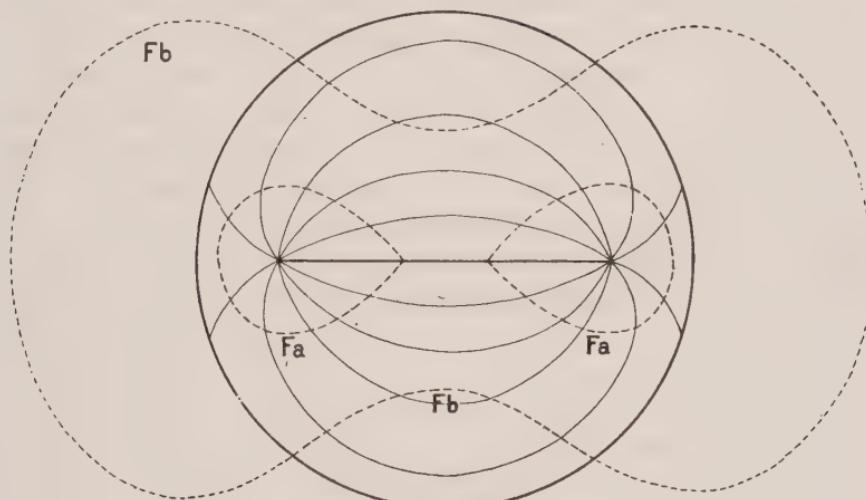


Fig. 97.

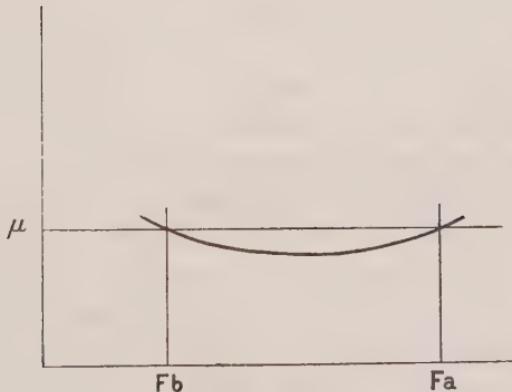


Fig. 98.

in the region intermediate to the two dotted curves, it will tend to move towards regions of weaker field-strength.

The locus F_b is therefore a locus of stable position, towards which the body tends to move; the locus F_a is a locus of unstable position, from which it tends to move. If the body were placed across F_a ,

it might be torn asunder into two portions, the split coinciding with the locus F_a .

Suppose a number of such bodies to be scattered throughout the medium. Let at first the regions F_a and F_b be entirely outside the space where the bodies are situated: and, in making this supposition we may, if we please, suppose that the loci which we are calling F_a and F_b are meanwhile situated somewhat farther from the axis than in our figure, that (for instance) F_a is situated where we have drawn F_b , and that F_b is still farther out. The bodies then tend towards the poles; but the tendency may be very small if, in Fig. 98, the curve and its intersecting straight line do not diverge very far from one another beyond F_a ; in other words, if, when

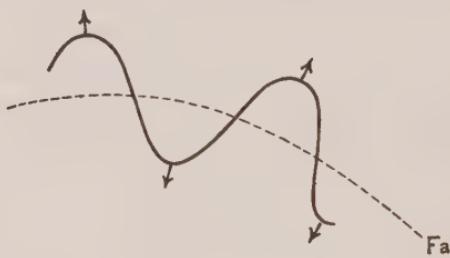


Fig. 99.

situated in this region, the permeability of the bodies is not very much in excess of that of the medium.

Let the poles now tend to separate farther and farther from one another, the strength of each pole remaining unaltered; in other words, let the centrosome-foci recede from one another, as they actually do, drawing out the spindle-threads between them. The loci F_a , F_b will close in to nearer relative distances from the poles. In doing so, when the locus F_a crosses one of the bodies, the body may be torn asunder; if the body be of elongated shape, and be crossed at more points than one, the forces at work will tend to exaggerate its foldings, and the tendency to rupture is greatest when F_a is in some median position (Fig. 99).

When the locus F_a has passed entirely over the body, the body tends to move towards regions of weaker force; but when, in turn, the locus F_b has crossed it, then the body again moves towards regions of stronger force, that is to say, towards the nearest pole.

And, in thus moving towards the pole, it will do so, as appears actually to be the case in the dividing cell, along the course of the outer lines of force, the so-called "mantle-fibres" of the histologist*.

Such considerations as these give general results, easily open to modification in detail by a change of any of the arbitrary postulates which have been made for the sake of simplicity. Doubtless there are other assumptions which would meet the case; for instance, that during the active phase of the chromatin molecule (when it decomposes and sets free nucleic acid) it carries a charge opposite to that which it bears during its resting, or alkaline phase; and that it would accordingly move towards different poles under the influence of a current, wandering with its negative charge in an alkaline fluid during its acid phase to the anode, and to the cathode during its alkaline phase. A whole field of speculation is opened up when we begin to consider the cell not merely as a polarised electrical field, but also as an electrolytic field, full of wandering ions. Indeed it is high time we reminded ourselves that we have perhaps been dealing too much with ordinary physical analogies: and that our whole field of force within the cell is of an order of magnitude where these grosser analogies may fail to serve us, and might even play us false, or lead us astray. But our sole object meanwhile, as I have said more than once, is to demonstrate, by such illustrations as these, that, whatever be the actual and as yet unknown *modus operandi*, there are physical conditions and distributions of force which could produce just such phenomena of movement as we see taking place within the living cell. This, and no more, is precisely what Descartes is said to have claimed for his description of the human body as a "mechanism†."

While it can scarcely be too often repeated that our enquiry is not directed towards the solution of physiological problems, save only in so far as they are inseparable from the problems presented by the visible configurations of form and structure, and while we try, as far as possible, to evade the difficult question of what

* We have not taken account in the above paragraphs of the obvious fact that the supposed symmetrical field of force is distorted by the presence in it of the more or less permeable bodies; nor is it necessary for us to do so, for to that distorted field the above argument continues to apply, word for word.

† Michael Foster, *Lectures on the History of Physiology*, 1901, p. 62.

particular forces are at work when the mere visible forms produced are such as to leave this an open question, yet in this particular case we have been drawn into the use of electrical analogies, and we are bound to justify, if possible, our resort to this particular mode of physical action. There is an important paper by R. S. Lillie, on the "Electrical convection of certain free cells and nuclei*", which, while I cannot quote it in direct support of the suggestions which I have made, yet gives just the evidence we need in order to shew that electrical forces act upon the constituents of the cell, and that their action discriminates between the two species of colloids represented by the cytoplasm and the nuclear chromatin. And the difference is such that, in the presence of an electrical current, the cell substance and the nuclei (including sperm-cells) tend to migrate, the former on the whole with the positive, the latter with the negative stream: a difference of electrical potential being thus indicated between the particle and the surrounding medium, just as in the case of minute suspended particles of various kinds in various feebly conducting media†. And the electrical difference is doubtless greatest, in the case of the cell constituents, just at the period of mitosis: when the chromatin is invariably in its most deeply staining, most strongly acid, and therefore, presumably, in its most electrically negative phase. In short, Lillie comes easily to the conclusion that "electrical theories of mitosis are entitled to more careful consideration than they have hitherto received."

* *Amer. J. Physiol.* viii, pp. 273-283, 1903 (*vide supra*, p. 314); cf. *ibid.* xv, pp. 46-84, 1905; xxii, p. 106, 1910; xxvii, p. 289, 1911; *Journ. Exp. Zool.* xv, p. 23, 1913; etc.

† In like manner Hardy shewed that colloid particles migrate with the negative stream if the reaction of the surrounding fluid be alkaline, and *vice versa*. The whole subject is much wider than these brief allusions suggest, and is essentially part of Quincke's theory of Electrical Diffusion or Endosmosis: according to which the particles and the fluid in which they float (or the fluid and the capillary wall through which it flows) each carry a charge: there being a discontinuity of potential at the surface of contact and hence a field of force leading to powerful tangential or shearing stresses, communicating to the particles a velocity which varies with the density per unit area of the surface charge. See W. B. Hardy's paper on Coagulation by electricity, *Journ. Physiol.* xxiv, pp. 288-304, 1899; also Hardy and H. W. Harvey, Surface electric charges of living cells, *Proc. R.S. (B)*, lxxxiv, pp. 217-226, 1911, and papers quoted therein. Cf. also E. N. Harvey's observations on the convection of unicellular organisms in an electric field (Studies on the permeability of cells, *Journ. Exp. Zool.* x, pp. 508-556, 1911).

Among other investigations all leading towards the same general conclusion, namely that differences of electric potential play their part in the phenomena of cell division, I would mention a noteworthy paper by Ida H. Hyde*, in which the writer shews (among other important observations) that not only is there a measurable difference of potential between the animal and vegetative poles of a fertilised egg (*Fundulus*, toad, turtle, etc.), but also that this difference fluctuates, or actually reverses its direction, periodically, at epochs coinciding with successive acts of segmentation or other

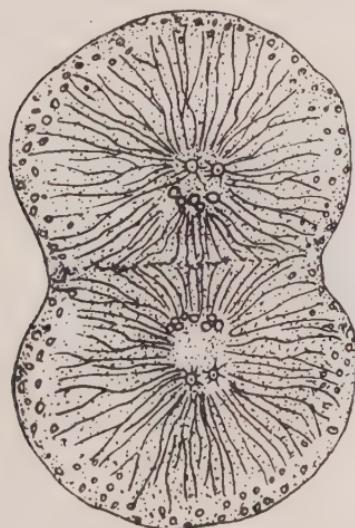


Fig. 100. Final stage in the first segmentation of the egg of *Cerebratulus*. From Prenant, after Coe*.

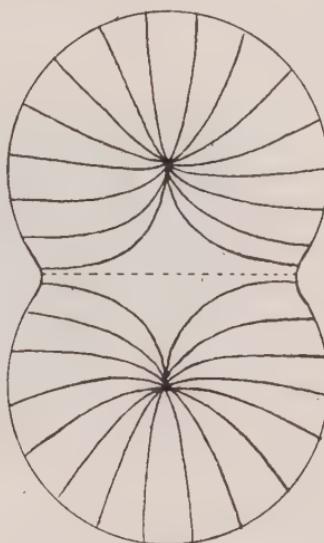


Fig. 101. Diagram of field of force with two similar poles.

important phases in the development of the egg†; just as other physical rhythms, for instance, in the production of CO_2 , had already been shewn to do. Hence we need not be surprised to find that the "materialised" lines of force, which in the earlier stages form the

* On differences in electrical potential in developing eggs, *Amer. Journ. Physiol.* xii, pp. 241–275, 1905. This paper contains an excellent summary, for the time being, of physical theories of the segmentation of the cell.

† Gray has demonstrated a temporary increase of electrical conductivity in sea-urchin eggs during the process of fertilisation, and ascribes the changes in resistance to polarisation of the surface: Electrical conductivity of echinoderm eggs, etc., *Phil. Trans. (B)*, ccvii, pp. 481–529, 1916.

convergent curves of the spindle, are replaced in the later phases of caryokinesis by divergent curves, indicating that the two foci, which are marked out in the field by the divided and reconstituted nuclei, are now alike in their polarity* (Figs. 100, 101).

The foregoing account is based on the provisional assumption that the phenomena of caryokinesis are analogous to those of a bipolar electrical field—a comparison which seems to offer a helpful and instructive series of analogies. But there are other forces which lead to similar configurations. For instance, some of Leduc's diffusion-experiments offer very remarkable analogies to the diagrammatic phenomena of caryokinesis, as shewn in Fig. 102†.

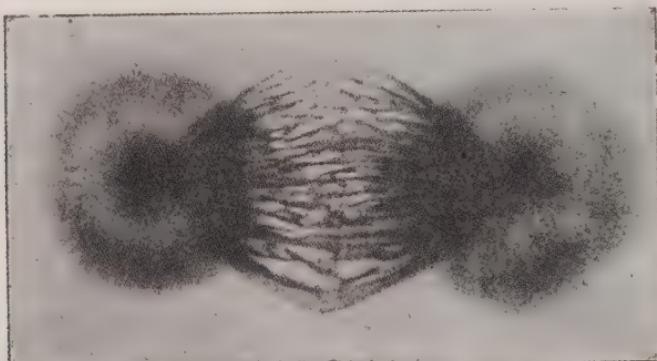


Fig. 102. Artificial caryokinesis (after Leduc), for comparison with Fig. 88, p. 299.

Here we have two identical (not opposite) poles of osmotic concentration, formed by placing a drop of Indian ink in salt water, and then on either side of this central drop, a hypertonic drop of salt solution more lightly coloured. On either side the pigment of the central drop has been drawn towards the focus nearest to it; but in the middle line, the pigment is drawn in opposite directions by equal forces, and so tends to remain undisturbed, in the form of an "equatorial plate."

To account for the same mitotic phenomena an elegant hypothesis has been put forward by A. B. Lamb‡, and developed by Graham

* W. R. Coe, Maturation and fertilisation of the egg of *Cerebratulus*, *Zool. Jahrbücher (Anat. Abth.)*, XII, pp. 425–476, 1899.

† *Op. cit.* pp. 110 and 91.

‡ A. B. Lamb, A new explanation of the mechanism of mitosis, *Journ. Exp. Zool.* v, pp. 27–33, 1908.

Cannon*. It depends on certain investigations of the Bjerknes, father and son†, which prove that bodies pulsating or oscillating‡ in a fluid set up a field of force precisely comparable with the lines of force in a magnetic field. Certain old and even familiar observations had pointed towards this phenomenon. Guyot had noticed that bits of paper were attracted towards a vibrating tuning-fork; and Schellbach found that a sounding-board so acts on bodies in its neighbourhood as to attract those which are heavier and repel those which are lighter than the surrounding medium; in air bits of paper are attracted and a gas-flame is repelled. To explain these simple observations, Bjerknes experimented with little drums attached to an automatic bellows. He found that two bodies in a fluid field, synchronously pulsating or synchronously oscillating, repel one another when their oscillations are in the same phase, or their pulsations are in opposite phase; and *vice versa*: while other particles, floating passively in the same fluid, tend (as Schellbach had observed before) to be attracted or repulsed according as they are heavier or lighter than the fluid medium. The two bodies behave towards one another like two electrified bodies, or like two poles of a magnet; we are entitled to speak of them as "hydrodynamic poles," we might even call them "hydrodynamic magnets"; and pursuing the analogy, we may call the heavy bodies paramagnetic, and the light ones diamagnetic with regard to them. Lamb's hypothesis then, and Cannon's, is that the centrosomes act as "hydrodynamic magnets." The explanation depends on oscillations which have never been seen, in centrosomes which are not always to be discovered. But it brings together certain curious analogies, and these, where we know so little, may be worth reflecting on.

If we assume that each centrosome is endowed with a vibratory motion as it floats in the semi-fluid colloids, or hydrosols (to use Graham's word) of the cell, we may take it that the visible intracellular phenomena will be much the same as those we have

* *Op. cit.* Cf. also Gertrud Woken, *Zur Physik der Kernteilung*, *Z. f. allg. Physiol.* XVIII, pp. 39–57, 1918.

† V. Bjerknes, *Vorlesungen über hydrodynamische Fernkräfte, nach C. A. Bjerknes' Theorie*, Leipzig, 1900.

‡ A body is said to pulsate when it undergoes a rhythmic change of volume; it oscillates when it undergoes a rhythmic change of place.

described under an electrical hypothesis; the lines of force will have the same distribution, and such movements as the chromosomes undergo, and such symmetrical configurations as they assume, may be accounted for under the one hypothesis pretty much as under the other. There are however other phenomena accompanying mitosis, such as Chambers's astral currents and certain local changes in the viscosity of the egg, which are more easily explained by the hydrodynamic theory.

We may assume that the cytoplasm, however complex it may be, is but a sort of microscopically homogeneous emulsion of high dispersion, that is to say one in which the minute particles of one phase are widely scattered throughout, and freely mobile in, the other; and this indeed is what is meant by calling it a *hydrosol*. Let us assume also that the particles are a little less dense than the continuous phase in which they are dispersed; and assume lastly (it is not the easiest of our assumptions) that these ultra-minute particles will be affected, just as are the grosser ones, by the forces of the hydrodynamic field.

All this being so, the disperse particles will be repelled from the oscillating centrosome, with a force which falls off very rapidly, for Bjerknes tells us that it varies inversely as the seventh power of the distance; a round clear field, like a drop or a bubble, will be formed round the centrosome; and the disperse particles, expelled from this region, will tend to accumulate in a crowded spherical zone immediately beyond it. Outside of this again they will continue to be repulsed, but slowly, and we may expect a second and lesser concentration at the periphery of the cell. A clear central mass, or "centrosphere," will thus come into being; and the surrounding cytoplasm will be rendered denser and more viscous, especially close around the centrosphere and again peripherally, by condensation of the disperse particles. Moreover, all outward movements of these lighter particles entail inward movements of the heavier, which (by hypothesis) are also the more fluid; stream-lines or visible currents will flow towards the centre, giving rise to the star-shaped "aster," and the best accounts of the sea-urchin's egg* tally well with what is thus deduced from the hydrodynamic

* Cf. R. Chambers, in *Journ. Exp. Zool.* xxiii, p. 483, 1917; *Trans. R.S. Canada*, xii, 1918; *Journ. Gen. Physiol.* II, 1919.

hypothesis. The round drop of clear fluid which forms the centre of the aster grows as the aster grows, fluid streaming towards it from all parts of the cell along the channels of the astral rays. The cytoplasm between the rays is in the *gel* state, but gradually passes into a *sol* beyond the confines of the aster. Seifritz asserts that the substance of the centrosphere is "not much more viscous than water," but that the wedges of cytoplasm between the inwardly directed streams are stiff and viscous*.

After the centrosome divides we have two oscillating bodies instead of one; they tend to repel one another, and pass easily through the fluid centrosphere to the denser layer around. But now the new centrosomes, on opposite sides of the centrosphere, repel, each on its own side, the disperse particles of the denser zone; and two new asters are formed, their rays marked by the streams coursing inwards to the centrosome-foci. Thus the *amphiaster* comes into being; it is not that the old aster divides, as a definite entity; but the old aster ceases to exist when its focus is disturbed, and about the new foci new asters are necessarily and automatically developed. Again this hypothetic account tallies well with Chambers's description.

The same attractions and repulsions should be manifested, perhaps better still, in whatsoever bodies lie or float within the cell, whether liquid or solid, oil-globules, yolk-particles, mitochondria, chromosomes or what not. A zoned, concentric arrangement of yolk-globules is often seen in the egg, with the centrosome as focus; and in certain sea-urchin eggs the mitochondria gather around the centrosome while the amphiaster is forming, collecting together in that very zone to which Chambers ascribes a semi-rigid or viscous consistency†. The Golgi bodies found in various germ-cells are at first black rod-like bodies embedded in the centrosphere; they undergo changes and complex movements, now scattering through the cytoplasm and anon crowding again around the centrosome. Some periodic change in the density of these bodies compared with

* Cf. W. Seifritz, Some physical properties of protoplasm, *Ann. Bot.* xxxv, 1921. Wo. Ostwald and M. H. Fischer had thought that the astral rays were due to local changes of the plasma-sol into a gel, *Zur physikal. chem. Theorie der Befruchtung, Pflüger's Archiv*, cvi, pp. 229–266, 1905.

† Cf. F. Vejdovsky and A. Mrazek, Umbildung des Cytoplasma während der Befruchtung und Zelltheilung, *Arch. f. mikr. Anat.* LXII, 431–579, 1903.

that of the medium in which they lie seems all that is required to account for their excursions; and such changes of density are not only of likely occurrence during the active chemical operations associated with fertilisation and division, but are in all probability inseparable from the changes in viscosity which are known to occur*. The movements and arrangements of the chromosomes, already described, may be easily accounted for if we postulate, in addition to their repulsion from the oscillating centrosomes, induced oscillations in themselves such as to cause them to attract one another.

The well-defined length of the spindle and the position of equilibrium in which it comes to rest may be conceived as resultants of the several mutual repulsions of the centrosomes by one another, by the chromosomes or other lighter material of the equatorial plate, and again by such lighter material as may have accumulated at the periphery of the egg; the first two of these will tend to lengthen the spindle, the last to shorten it; and the last will especially affect its position and direction. When Chambers amputated part of an amphistastral egg, the remains of the amphiaster disappeared, and then came into being again in a new and more symmetrical position; it or its centrosomal focus had been symmetrically repelled, we may suppose, by the fresh surface. Hertwig's law that the spindle-axis tends to lie in the direction of the largest mass of protoplasm, in other words to point where the cell-surface lies farthest off and its repulsion is least felt, may likewise find its easy explanation.

Between these hypotheses we may choose one or other (if we choose at all), according to our judgment. As Henri Poincaré tells us, we never know that any one physical hypothesis is *true*, we take the simplest we can find; and this we call the guiding principle of simplicity! In this case, the hydrodynamic hypothesis is a simple one; but it all rests on a hypothetic oscillation of the centrosomes, which has never been witnessed. Bayliss has shewn that precisely such reversible states of gelation as we have been speaking of as

* Cf. G. Odquist, Viscositätsänderungen des Zellplasmas während der ersten Entwicklungsstufen des Froscheis, *Arch. f. Entw. Mech.* LI, pp. 610-624, 1922; A. Gurwitsch, Prämissen und anstossgebende Faktoren der Furchung und Zelltheilung, *Arch. f. Zellforsch.* II, pp. 495-548, 1909; L. V. Heilbrunn, Protoplasmic viscosity-changes during mitosis, *Journ. Exp. Zool.* XXXIV, pp. 417-447, 1921; *ibid.* XLIV, pp. 255-278, 1926; E. Leblond, Passage de l'état de gel à l'état de sol dans le protoplasme vivant, *C.R. Soc. Biol.* LXXXII, p. 1150; cf. *ibid.* p. 1220; etc.

"periodic changes in viscosity" may be induced in living protoplasm by electrical stimulation*. On the other hand, the fact that the hydrodynamic forces fall off as fast as they do with increasing distance limits their efficacy; and the minute disperse particles must, under Stokes's law, be slow to move. Lastly, it may well be (as Lillie has urged) that such work as his own, or Ida Hyde's, or Gray's, on change of potential in developing eggs, taken together with that of many others on the behaviour of colloid particles in an electrical field, has not yet been followed out in all its consequences, either on the physical or the physiological side of the problem.

But to return to our general discussion.

As regards the actual mechanical division of the cell into two halves, we shall see presently that, in certain cases, such as that of a long cylindrical filament, surface-tension, and what is known as the principle of "minimal areas," go a long way to explain the mechanical process of division; and in all cells whatsoever, the process of division must somehow be explained as the result of a conflict between surface-tension and its opposing forces. But in such a case as our spherical cell, it is none too easy to see what physical cause is at work to disturb its equilibrium and its integrity.

The fact that when actual division of the cell takes place, it does so at right angles to the polar axis and precisely in the direction of the equatorial plane, would lead us to suspect that the new surface formed in the equatorial plane sets up an annular tension, directed inwards, where it meets the outer surface layer of the cell itself. But at this point the problem becomes more complicated. Before we can hope to comprehend it, we shall have not only to enquire into the potential distribution at the surface of the cell in relation to that which we have seen to exist in its interior, but also to take account of the differences of potential which the material arrangements along the lines of force must themselves tend to produce. Only thus can we approach a comprehension of the balance of forces which cohesion, friction, capillarity and electrical distribution combine to set up.

The manner in which we regard the phenomenon would seem to

* W. M. Bayliss, Reversible gelation in living protoplasm, *Proc. R.S. (B)*, xci, pp. 196-201, 1920.

turn, in great measure, upon whether or no we are justified in assuming that, in the liquid surface-film of a minute spherical cell, local and symmetrically localised differences of surface-tension are likely to occur. If not, then changes in the conformation of the cell such as lead immediately to its division must be ascribed not to local changes in its surface-tension, but rather to direct changes in internal pressure, or to mechanical forces due to an induced surface-distribution of electrical potential. We have little reason to be sceptical; in fact we now know that the cell is so far from being chemically and physically homogeneous that local variations in its surface-tension are more than likely, they are certain to occur.

Bütschli suggested more than sixty years ago that cell-division was brought about by an increase of surface-tension in the equatorial region of the cell; and the suggestion was the more remarkable that it was (I believe) the very first attempt to invoke surface-tension as a factor in the physical causation of a biological phenomenon*. An increase of equatorial tension would cause the surface-area there to diminish, and the equator to be pinched in; but the total surface-area of the cell would be increased thereby, and the two effects would strike a balance†. But, as Bütschli knew very well, the surface-tension change would not stand alone; it would bring other phenomena in its train, currents would tend to be set up, and tangential strains would be imposed on the cell-membrane or cell-surface as a whole. The secondary if not the direct effects of increased equatorial tension might, after all, suffice for the division of the cell. It was Loeb, in 1895, who first shewed that streaming went on from the equator towards the divided nuclei. To the violence of these streaming movements he attributed the phenomenon of division, and many other physiologists have adopted this hypothesis‡. The currents of which Loeb spoke call for counter-currents

* O. Bütschli, Über die ersten Entwicklungsorgänge der Eizelle, *Abh. Senckenberg. naturf. Gesellsch.* x, 1876; Über Plasmastromungen bei der Zelltheilung, *Arch. f. Entw. Mech.* x, p. 52, 1900. Ryder ascribed the caryokinetic figures to surface-tension in his *Dynamics in Evolution*, 1894.

† A relative, not positive, increase of surface-tension, was part of Giardina's hypothesis: Note sul mecanismo della divisione cellulare, *Anat. Anz.* xxii, 1902.

‡ J. Loeb, *Amer. Journ. Physiol.* vi, p. 432, 1902; E. G. Conklin, Protoplasmic movements as a factor in differentiation, *Wood's Hole Biol. Lectures*, p. 69, etc., 1898-99; J. Spek, Oberflächenspannungsdifferenzen als eine Ursache der Zellteilung, *Arch. f. Entw. Mech.* XLIV, pp. 54-73, 1918.

towards the equator, in or near the surface of the cell; and theory and observation both indicate that precisely such currents are bound to be set up by the surface-energy involved in the increase of equatorial tension.

An opposite view has been held by some, and especially by T. B. Robertson*. Quincke had shewn that the formation of soap at the surface of an oil-droplet lowers the surface-tension of the latter, and that if the saponification be local, that part of the surface tends to enlarge and spread out accordingly. Robertson, in a very curious experiment, found that by laying a thread, moistened with dilute caustic alkali or merely smeared with soap, across a drop of olive oil afloat in water, the drop at once divided into two. A vast amount of controversy has arisen over this experiment, but Spek seems to have shewn conclusively that it is an exceptional case.

In a drop of olive-oil, balanced in water† and touched *anywhere* with an alkali, there is so copious a formation of lighter soaps that differences of density tend to drag the drop in two. But in the case of other oils (and especially the thinner oils, such as oil of bergamot) the saponified portion bulges, as theory directs; and when the alkali is applied to two opposite poles the equatorial region is pinched in, as McClendon‡, in opposition to Robertson, had found it to do. Conversely, if an alkaline thread be looped around the drop, the zone of contact bulges, and instead of dividing at the equator the drop assumes a lens-like form.

We may take it then as proven that a relative increase of equatorial surface-tension, whether in oil-drops, mercury-globules or living cells, does lead, or tend to lead, to an equatorial constriction. In all cases a system of surface-currents is set up among the fluid drops towards the zone of increased tension; and an axial counter-current flows towards the pole or poles of lowered tension. Precisely such currents have been observed to run in various eggs (especially of

* T. B. Robertson, Note on the chemical mechanics of cell-division, *Arch. f. Entw. Mech.* xxvii, p. 29, 1909; xxxii, p. 308, 1911; xxxv, p. 402, 1913. Cf. R. S. Lillie, *Journ. Exp. Zool.* xxi, pp. 369–402, 1916; McClendon, *loc. cit.*; etc.

† In these experiments, and in many of Quincke's, a little chloroform is added to the oil, in order to bring its density as near as may be to that of water.

‡ J. F. McClendon, Note on the mechanics of cell-division, *Arch. f. Entw. Mech.* xxxiv, pp. 263–266, 1912.

certain Nematodes) during division of the cell; but if the process be slow, more than 7 or 8 minutes long, the slow currents become hard to see. Various contents of the cell are transported by these currents, and clear, yolk-free polar caps and equatorial accumulations of yolk and pigment are among the various manifestations of the phenomenon. The extrusion of a polar body, at a small and sharply defined region of lowered tension, is a particular case of the same principle*.

But purely chemical changes are not of necessity the fundamental cause of alteration in the surface-tension of the egg, for the action of electrolytes on surface-tension is now well known and easily demonstrated. So, according to other views than those with which we have been dealing, electrical charges are sufficient in themselves to account for alterations of surface-tension, and in turn for that protoplasmic streaming which, as so many investigators agree, initiates the segmentation of the egg†. A great part of our difficulty arises from the fact that in such a case as this the various phenomena are so entangled and apparently concurrent that it is hard to say which initiates another, and to which this or that secondary phenomenon may be considered due. Of recent years the phenomenon of *adsorption* has been adduced (as we have already briefly said) in order to account for many of the events and appearances which are associated with the asymmetry, and lead towards the division, of the cell. But our short discussion of this phenomenon may be reserved for another chapter.

However, we are not directly concerned here with the phenomena of segmentation or cell-division in themselves, except only in so far as visible changes of form are capable of easy and obvious correlation with the play of force. The very fact of "development" indicates that, while it lasts, the equilibrium of the egg is never complete‡. And the gist of the matter is that, if you have caryokinetic figures developing inside the cell, that of itself indicates that the dynamic system and the localised forces arising from it are in

* J. Spek, *loc. cit.* pp. 108–109.

† Cf. D'Arsonval, *Relation entre la tension superficielle et certains phénomènes électriques d'origine animale*, *Arch. de Physiol.* 1, pp. 460–472, 1889; Ida H. Hyde, *op. cit.* p. 242.

‡ Cf. Plateau's remarks (*Statique des liquides*, II, p. 154) on the tendency towards equilibrium, rather than actual equilibrium, in many of his systems of soap-films.

gradual alteration; and changes in the outward configuration of the system are bound, consequently, to take place.

Perhaps we may simplify the case still more. We have learned many things about cell-division, but we do not know much in the end. We have dealt, perhaps, with too many related phenomena, and failed because we tried to combine and account for them all. A physical problem, still more a mathematical one, wants reducing to its simplest terms, and Dr Rashevsky has simplified and generalised the problem of cell-division (or division of a drop) in a series of papers, which still outrun by far the elementary mathematics of this book. If we cannot follow him in all he does, we may find useful lessons in his way of doing it. Cells are of many kinds; they differ in size and shape, in visible structure and chemical composition. Most have a nucleus, some few have none; most need oxygen, some few do not; some metabolise in one way, some in another. What small residuum of properties remains common to them all? A living cell is a little fluid (or semi-fluid) system, in which work is being done, physical forces are in operation and chemical changes are going on. It is in such intimate relation with the world outside—its own *milieu interne* with the great *milieu externe*—that substances are continually entering the cell, some to remain there and contribute to its growth, some to pass out again with loss of energy and metabolic change. The picture seems simplicity itself, but it is less simple than it looks. For on either side of the boundary-wall, both in the adjacent medium and in the living protoplasm within, there will be no uniformity, but only degrees of activity, and *gradients of concentration*. Substances which are being absorbed and consumed will diminish from periphery to centre; those which are diffusing outwards have their greatest concentration near the centre, decrease towards the periphery, and diminish further with increasing distance in the near neighbourhood of the system. Size, shape, diffusibility, permeability, chemical properties of this and that, may affect the gradients, but in the living cell the interchanges are always going on, and the *gradients* are always there*.

* Outward diffusion makes one of the many contrasts between cell-growth and crystal-growth. But the diffusion-gradients round a growing crystal are far more complicated than was once supposed. Cf. W. F. Berg, Crystal growth from solutions, *Proc. R.S. (A)*, CLXIV, pp. 79–95, 1938.

If the cell be homogeneous, taking in and giving out at a constant rate in a uniform way, its shape will be spherical, the concentration-field of force, or concentration-field, will likewise have a spherical symmetry, and the resultant force will be zero. But if the symmetry be ever so little disturbed, and the shape be ever so little deformed, then there will be forces at work tending to increase the deformation, and others tending to equalise the surface-tension and restore the spherical symmetry, and it can be shewn that such agencies are within the range of the chemistry of the cell. Since surface-tension becomes more and more potent as the size of the drop diminishes, it follows that (under fluid conditions) the smallest solitary cells are least likely to depart from a spherical shape, and that cell-division is only likely to occur in cells above a certain critical order of magnitude; and using such physical constants as are available, Rashevsky finds that this critical magnitude tallies fairly well with the average size of a living cell. The more important lesson to learn, however, is this, that, merely *by virtue of its metabolism*, every cell contains within itself factors which may lead to its division after it reaches a certain critical size.

There are simple corollaries to this simple setting of the case. Since unequal concentration-gradients are the chief cause which renders non-spherical shapes of cell possible, and these last only so long as the cell lives and metabolises, it follows that, as soon as the gradients disappear, whether in death or in a "resting-stage", the cell reverts to a spherical shape and symmetry. Again, not only is there a critical size above which cell-division becomes possible, and more and more probable, but there must also be a size beyond which the cell is not likely to grow. For the "specific surface" decreases, the metabolic exchanges diminish, the gradients become less steep, and the rate of growth decreases too; there must come a stage where anabolism just balances katabolism, and growth ceases though life goes on. When streaming currents are visible within the cell, they seem to complicate the problem; but after all, they are part of the result, and proof of the existence, of the gradients we have described. In any further account of Rashevsky's theories the mathematical difficulties very soon begin. But it is well to realise that pure theory often carries the mathematical physicist a long way; and that higher and higher powers of the microscope, and

greater and greater histological skill are not the one and only way to study the physical forces acting within the cell*.

As regards the phenomena of fertilisation, of the union of the spermatozoon with the "pronucleus" of the egg, we might study these also in illustration, up to a certain point, of the forces which are more or less manifestly at work. But we shall merely take, as a single illustration, the paths of the male and female pronuclei, as they travel to their ultimate meeting-place.

The spermatozoon, when within a very short distance of the egg-cell, is attracted by it, the same attraction being further manifested in a small conical uprising of the surface of the egg†. The nature of the attractive force has been much disputed. Loeb found the spermatozoon to be equally attracted by other substances, even by a bead of glass. It has been held also that the attraction is chemotropic, some substance being secreted by the egg which drew the sperm towards it: just as Pfeffer, having shewn that malic acid has an attraction for fern-antheridia, supposed this substance to play its attractive part within the mucus of the archegonia. Again, the chemical secretion may be neither attractive nor directive, but yet play a useful part in activating the spermatozoa. However that may be, Gray has shewn reason to believe that an electromotive force is developed in the contact between active spermatozoon and inactive ovum; and that it is the electrical change so set up, and almost instantaneously propagated, which precludes the entry of another spermatozoon‡. Whatever the force may be, it is one which acts normally to the surface of the ovum, and after entry the

* Cf. N. Rashevsky, *Mathematical Biophysics*, Chicago, 1938; and many earlier papers. E.g. Physico-mathematical aspects of cellular multiplication and development, *Cold Spring Harbor Symposia*, ii, 1934; The mechanism of division of small liquid systems which are the seat of physico-chemical reactions, *Physics*, III, pp. 374-379, 1934; papers in *Protoplasma*, XIV-XX, 1931-33, etc.

† With the classical account by H. Fol, *C.R.* LXXXIII, p. 667, 1876; *Mém. Soc. Phys. Genève*, xxvi, p. 89, 1879, cf. Robert Chambers, The mechanism of the entrance of sperm into the star-fish egg, *Journ. Gen. Physiol.* v, pp. 821-829, 1923. Here a delicate filament is said to run out from the fertilisation-cone and drag the spermatozoon in; but this is disputed and denied by E. Just, *Biol. Bull.* LVII, pp. 311-325, 1929.

‡ But, under artificial conditions, "polyspermny" may take place, e.g. under the action of dilute poisons, or of an abnormally high temperature, these being doubtless also conditions under which the surface-tension is diminished.

spermatozoon points straight towards the centre of the egg. From the fact that other spermatozoa, subsequent to the first, fail to effect an entry, we may safely conclude that an immediate consequence of the entry of the spermatozoon is an increase in the surface-tension of the egg: this being but one of the complex reactions exhibited by the surface, or cortex of the cell*. Somewhere or other, within the egg, near or far away, lies its own nuclear body, the so-called female pronucleus, and we find that after a while this has fused with the "male pronucleus" or head of the spermatozoon, and that the body resulting from their fusion has come to occupy the centre of the egg. This *must* be due (as Whitman pointed out many years ago) to a force of attraction acting between the two bodies, and another force acting upon one or other or both in the direction of the centre of the cell. Did we know the magnitude of these several forces, it would be an easy task to calculate the precise path which the two pronuclei would follow, leading to conjugation and to the central position. As we do not know the magnitude, but only the direction, of these forces, we can only make a general statement: (1) the paths of both moving bodies will lie wholly within a plane triangle drawn between the two bodies and the centre of the cell; (2) unless the two bodies happen to lie, to begin with, precisely on a diameter of the cell, their paths until they meet one another will be curved paths, the convexity of the curve being towards the straight line joining the two bodies; (3) the two bodies will meet a little before they reach the centre; and, having met and fused, will travel on to reach the centre in a straight line. The actual study and observation of the path followed is not very easy, owing to the fact that what we usually see is not the path itself, but only a *projection* of the path upon the plane of the microscope; but the curved path is particularly well seen in the frog's egg, where the path of the spermatozoon is marked by a little streak of brown pigment, and the fact of the meeting of the pronuclei before reaching the centre has been repeatedly seen by many observers†.

* See Mrs Andrews' beautiful observations on "Some spinning activities of protoplasm in starfish and echinoid eggs," *Journ. Morphol.* XII, pp. 307-389, 1897.

† W. Pfeffer, *Locomotorische Richtungsbewegungen durch chemische Reize*, *Unters. a. d. Botan. Inst. Tübingen*, I, 1884; *Physiology of Plants*, III, p. 345, Oxford, 1906; W. J. Dakin and M. G. C. Fordham, *Journ. Exp. Biol.* I, pp. 183-200, 1924. Cf. J. Loeb, *Dynamics of Living Matter*, 1906, p. 153.

The problem recalls the famous problem of three bodies, which has so occupied the astronomers; and it is obvious that the foregoing brief description is very far from including all possible cases. Many of these are particularly described in the works of Fol, Roux, Whitman and others*.

The intracellular phenomena of which we have now spoken have assumed great importance in biological literature and discussion during the last fifty years; but it is open to us to doubt whether they will be found in the end to possess more than a secondary, even a remote, biological significance. Most, if not all of them, would seem to follow immediately and inevitably from certain simple assumptions as to the physical constitution of the cell, and from an extremely simple distribution of polarised forces within it. We have already seen that how a thing grows, and what it grows into, is a dynamic and not a merely material problem; so far as the material substance is concerned, it is so only by reason of the chemical, electrical or other forces which are associated with it. But there is another consideration which would lead us to suspect that many features in the structure and configuration of the cell are of secondary biological importance; and that is, the great variation to which these phenomena are subject in similar or closely related organisms, and the apparent impossibility of correlating them with the peculiarities of the organism as a whole. In a broad and general way the phenomena are always the same. Certain structures swell and contract, twine and untwine, split and unite, advance and retire; certain chemical changes also repeat themselves. But Nature rings the changes on all the details. "Comparative study has shewn that almost every detail of the processes (of mitosis) described above is subject to variation in different forms of cells†." A multitude of cells divide to the accompaniment of caryokinetic phenomena; but others do so without any visible caryokinesis at all. Sometimes the polarised field of force is within,

* H. Fol, *Recherches sur la fécondation*, 1879; W. Roux, Beiträge zur Entwickelungsmechanik des Embryos, *Arch. f. Mikr. Anat.* xix, 1887; C. O. Whitman, Oökinesis, *Journ. Morph.* I, 1887; E. Giglio-Tos, Entwicklungsmechanische Studien, I, *Arch. f. Entw. Mech.* LI, p. 94, 1922. See also Frank R. Lillie, *Problems of Fertilisation*, Chicago, 1919.

† Wilson, *The Cell*, p. 77; cf. 3rd ed. (1925), p. 120.

sometimes it is adjacent to, and at other times it lies remote from, the nucleus. The distribution of potential is very often symmetrical and bipolar, as in the case described; but a less symmetrical distribution often occurs, with the result that we have, for a time at least, numerous centres of force, instead of the two main correlated poles: this is the simple explanation of the numerous stellate figures,

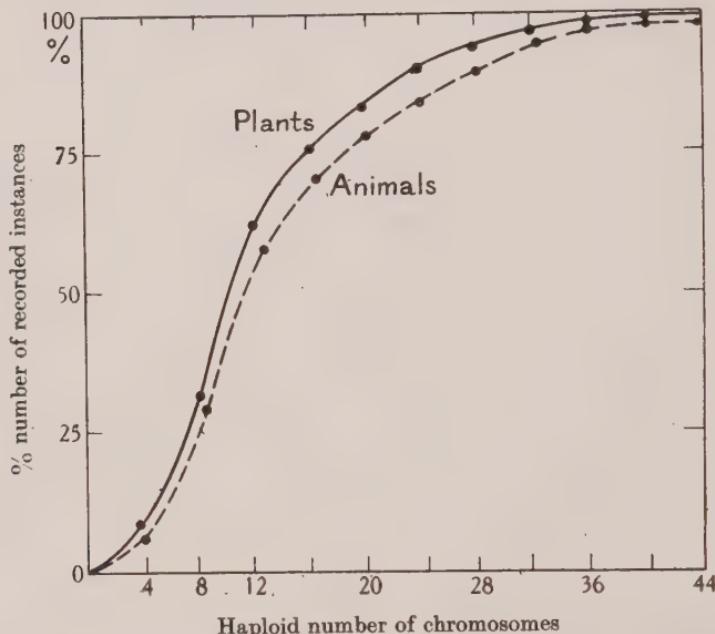


Fig. 103. Summation diagram shewing the % number of instances (among 2,415 phanerogams and 1,070 metazoa), in which the chromosomes do not exceed a given number. Data from M. J. D. White.

or "Strahlungen," which have been described in certain eggs, such as those of *Chaetopterus*. The number of chromosomes may be constant within a group, as in the tailed Amphibia, with 12; or very variable, as in sedges, and in grasshoppers*; in one and the same species of worm (*Ascaris megalcephala*), one group or two groups of chromosomes may be present. And remarkably constant, in general, as the number in any one species undoubtedly is, yet we must not forget that, in plants and animals alike, the whole range of observed numbers is but a small one (Fig. 103); for (as regards

* There are varieties of *Artemia salina* which hardly differ in outward characters, but differ widely in the number of their chromosomes.

the germ-nuclei) few have less than six chromosomes, and few have more than twenty*. In closely related animals, such as various species of Copepods, and even in the same species of worm or insect, the form of the chromosomes and their arrangement in relation to the nuclear spindle have been found to differ in ways alluded to above; while only here and there, as among the chrysanthemums, do related species or varieties shew their own characteristic chromosome numbers. In contrast to the narrow range of the chromosome numbers, we may reflect on the all but infinite possibilities of chemical variability. Miescher shewed that a molecule containing 40 C-atoms would admit (arithmetically though not necessarily chemically) of a million possible isomers; and changes in position of the N-atoms of a protein, for instance, might vastly increase that prodigious number. In short, we cannot help perceiving that many nuclear phenomena are not specifically related to the particular organism in which they have been observed, and that some are not even specially and indisputably connected with the organism as such. They include such manifestations of the physical forces, in their various permutations and combinations, as may also be witnessed, under appropriate conditions, in non-living things.

When we attempt to separate our purely morphological or "purely

* The commonest numbers of (haploid) chromosomes, both in plants and animals, are 8, 12 and 16. The median number is 12 in both, and the lower quartile is 8, likewise in both; but the upper quartile is 24 or thereby in animals, and in the neighbourhood of 16 in plants. If we may judge by the long lists given by E. B. Wilson (*The Cell*, 3rd ed. pp. 855-865), by M. Ishikawa in *Botan. Mag. Tokyo*, xxx, 1916, by M. J. D. White in his book on *Chromosomes*, or by Tischler in *Tabulae Biologicae* (1927), fully 60 per cent. of the observed cases lie between 6 and 16. As Wilson says (p. 866) "the number of chromosomes is *per se* a matter of secondary importance"; and (p. 868) "We must admit the present inadequacy of attempts to reduce the chromosome numbers to any single or consistent arithmetical rules." Clifford Dobell had said the same thing: "Nobody nowadays will be prepared to argue that chromosome numbers, as such, have any quantitative or qualitative relation to the characters exhibited by their owners. Complexity of bodily structure is certainly not correlated in any way with multiplicity of chromosomes"; *La Cellule*, xxxv, p. 188, 1924. On the other hand, Tischler stoutly maintains that chromosome-numbers give useful evidence of phylogenetic affinity (*Biol. Centralbl.* xlvi, pp. 321-345, 1928); and there are a few well-known cases, such as the chrysanthemums, where, undoubtedly, the numbers are constant and specific. Again in certain cases, the number of the chromosomes may differ in different *races* (diploid and tetraploid) of the same plant; and the difference is accompanied by differences in cell-size, in rate of growth, and even in the shape of the fruit (cf. Sinnott and Blakeslee, *Nat. Acad. of Sci.* 1938, p. 476).

embryological" studies from physiological and physical investigations, we tend *ipso facto* to regard each particular structure and configuration as an attribute, or a particular "character," of this or that particular organism. From this assumption we are easily led to the framing of theories as to the ancestral history, the classificatory position, the natural affinities of the several organisms: in fact, to apply our embryological knowledge to the study of *phylogeny*. When we find, as we are not long of finding, that our phylogenetic hypotheses become complex and unwieldy, we are nevertheless reluctant to admit that the whole method, with its fundamental postulates, is at fault; and yet nothing short of this would seem to be the case, in regard to the earlier phases at least of embryonic development. All the evidence at hand goes, as it seems to me, to shew that embryological data, prior to and even long after the epoch of segmentation, are essentially a subject for physiological and physical investigation and have but the slightest link, if any, with the problems of zoological classification. Comparative embryology has its own facts to classify, and its own methods and principles of classification. We may classify eggs according to the presence or absence, the paucity or abundance, of their associated food-yolk, the chromosomes according to their form and their number, the segmentation according to its various "types"—radial, bilateral, spiral, and so forth. But we have little right to expect, and in point of fact we shall very seldom and (as it were) only accidentally find, that these embryological categories coincide with the lines of "natural" or "phylogenetic" classification which have been arrived at by the systematic zoologist.

The efforts to explain "heredity" by help of "genes" and chromosomes, which have grown up in the hands of Morgan and others since this book was first written, stand by themselves in a category which is all their own and constitutes a science which is justified of itself. To weigh or criticise these explanations would lie outside my purpose, even were I fitted to attempt the task. When these great discoveries began to be made, Bateson crossed the ocean to see and hear for himself what Morgan and his pupils had to shew and to tell. He came home convinced, and humbly marvelling. And I leave this great subject on one side not because I doubt for a moment the facts nor dispute the hypotheses nor decry the im-

portance of one or other; but because we are so much in the dark as to the mysterious field of force in which the chromosomes lie, far from the visible horizon of physical science, that the matter lies (for the present) beyond the range of problems which this book professes to discuss, and the trend of reasoning which it endeavours to maintain.

The cell*, which Goodsir spoke of as a *centre of force*, is in reality a *sphere of action* of certain more or less localised forces; and of these, surface-tension is the particular force which is especially responsible for giving to the cell its outline and its morphological individuality. The partially segmented differs from the totally segmented egg, the unicellular Infusorian from the minute multi-

* The "cell-theory" began early and grew slowly. In a curious passage which Mr Clifford Dobell has shewn me (*Nov. Org.* II, 7, *ad fin.*), Bacon speaks of "cells" in the human body: of a "collocatio spiritus per corpoream molem, eiusque pori, meatus, venae et cellulae, et rudimenta sive tentamenta corporis organici." It is "surely one of the most strangely prophetic utterances which even Bacon ever made." Apart from this the story begins in the seventeenth century, with Robert Hooke's well-known figure of the "cells" in a piece of cork (1665), with Grew's "bladders" or "bubbles" in the parenchyma of young beans, and Malpighi's "utriculi" or "sacculi" in the parenchyma or "utricularum substantia" of various plants. Christian Fr. v. Wolff conceived, about the same time, a hypothetical "cell-theory," on the analogy of Leibniz's Monads; but the first clear idea of a cellular parenchyma, or *contextus cellularis*, came from C. Gottlieb Ludwig (1742), and from K. Fr. Wolff, who spoke freely of cells or *cellulae*. Fontana, author of a curious *Traité sur le venin de la vipère* (1781), described various histological elements, caught a glimpse of the nucleus, and experimented with reagents, using syrup of violets for a stain. Early in the eighteenth century the vessels of the plant played an important rôle, under Kurt Sprengel and Treviranus; but it was not till 1831 that Hugo v. Mohl recognised that they also arose from "cells." About this time Robert Brown discovered, or re-discovered, the nucleus (1833), which Schleiden called the *cytoblast*, or "cell-producer." It was Schleiden's idea, and a far-seeing one, that the cell lived a double life, a life of its own and the life of the plant to which it belonged: "jede Zelle führt nun ein zweifaches Leben: ein selbstständiges, nur ihrer eigenen Entwicklung angehörigen, und ein anderes mittelbares, insofern sie integrierender Theil einer Pflanze geworden ist" (*Phylogenesis*, 1838, p. 1). The cell-theory, so long a-building, may be said to have been launched, and christened, with Schwann's *Mikroskopische Untersuchungen* of 1839. Within the next five years Martin Barry shewed how cell-division starts with the nucleus, Henle described the budding of certain cells, and Goodsir declared that all cells originate in pre-existing cells, a doctrine at once accepted by Remak, and made famous in pathology by Virchow. (Cf. (*int. al.*) J. G. McKendrick, On the modern cell-theory, etc., *Proc. Phil. Soc. Glasgow*, xix, pp. 1-55, 1887; J. Stephenson, Robert Brown...and the cell-theory, *Proc. Linn. Soc.* 1931-2, pp. 45-54; M. Möbius, Hundert Jahre Zellenlehre, *Jen. Ztschr. LXXI*, pp. 313-326, 1938.)

cellular Turbellarian, in the intensity and the range of those surface-tensions which in the one case succeed and in the other fail to form a visible separation between the cells. Adam Sedgwick used to call attention to the fact that very often, even in eggs that appear to be totally segmented, it is yet impossible to discover an actual separation or cleavage, through and through, between the cells which on the surface of the egg are so clearly delimited; so far and no farther have the physical forces effectuated a visible "cleavage." The vacuolation of the protoplasm in *Actinophrys* or *Actinosphaerium* is due to localised surface-tensions, quite irrespective of the multi-nuclear nature of the latter organism. In short, the boundary walls due to surface-tension may be present or may be absent, with or without the delimitation of the other specific fields of force which are usually correlated with these boundaries and with the independent individuality of the cells. What we may safely admit, however, is that one effect of these circumscribed fields of force is usually such a separation or segregation of the protoplasmic constituents, the more fluid from the less fluid and so forth, as to give a field where surface-tension may do its work and bring a visible boundary into being. When the formation of a "surface" is once effected, its physical condition, or phase, will be bound to differ notably from that of the interior of the cell, and under appropriate chemical conditions the formation of an actual cell-wall, cellulose or other, is easily intelligible. To this subject we shall return again, in another chapter.

From the moment that we enter on a dynamical conception of the cell, we perceive that the old debates were vain as to what visible portions of the cell were active or passive, living or non-living. For the manifestations of force can only be due to the *interaction* of the various parts, to the transference of energy from one to another. Certain properties may be manifested, certain functions may be carried on, by the protoplasm apart from the nucleus; but the interaction of the two is necessary, that other and more important properties or functions may be manifested. We know, for instance, that portions of an Infusorian are incapable of regenerating lost parts in the absence of a nucleus, while nucleated pieces soon regain the specific form of the organism: and we are told that reproduction by fission cannot be *initiated*, though

apparently all its later steps can be carried on, independently of nuclear action. Nor, as Verworn pointed out, can the nucleus possibly be regarded as the "sole vehicle of inheritance," since only in the conjunction of cell and nucleus do we find the essentials of cell-life. "Kern und Protoplasma sind nur vereint lebensfähig," as Nussbaum said. Indeed we may, with E. B. Wilson, go further, and say that "the terms 'nucleus' and 'cell-body' should probably be regarded as only topographical expressions denoting two differentiated areas in a common structural basis."

Endless discussion has taken place regarding the centrosome, some holding that it is a specific and essential structure, a permanent corpuscle derived from a similar pre-existing corpuscle, a "fertilising element" in the spermatozoon, a special "organ of cell-division," a material "dynamic centre" of the cell, (as Van Beneden and Boveri call it); while on the other hand, it is pointed out that many cells live and multiply without any visible centrosomes, that a centrosome may disappear and be created anew, and even that under artificial conditions abnormal chemical stimuli may lead to the formation of new centrosomes. We may safely take it that the centrosome, or the "attraction sphere," is essentially a "centre of force," and that this dynamic centre may or may not be constituted by (but will be very apt to produce) a concrete and visible concentration of matter.

It is far from correct to say, as is often done, that the cell-wall, or cell-membrane, belongs "to the passive products of protoplasm rather than to the living cell itself"; or to say that in the animal cell, the cell-wall, because it is "slightly developed," is relatively unimportant compared with the important rôle which it assumes in plants. On the contrary, it is quite certain that, whether visibly differentiated into a semi-permeable membrane or merely constituted by a liquid film, the surface of the cell is the seat of important forces, capillary and electrical, which play an essential part in the dynamics of the cell. Even in the thickened, largely solidified cellulose wall of the plant-cell, apart from the mechanical resistances which it affords, the osmotic forces developed in connection with it are of essential importance.

But if the cell acts, after this fashion, as a whole, each part interacting of necessity with the rest, the same is certainly true of

the entire multicellular organism: as Schwann said of old, in very precise and adequate words, "the whole organism subsists only by means of the *reciprocal action* of the single elementary parts*." As Wilson says again, "the physiological autonomy of the individual cell falls into the background...and the apparently 'composite character which the multicellular organism may exhibit is owing to a secondary distribution of its energies among local centres of action†.'" It is here that the homology breaks down which is so often drawn, and overdrawn, between the unicellular organism and the individual cell of the metazoon‡.

Whitman, Adam Sedgwick§, and others have lost no opportunity of warning us against a too literal acceptation of the cell-theory, against the view that the multicellular organism is a colony (or, as Haeckel called it, in the case of the plant, a "republic") of independent units of life||. As Goethe said long ago, "Das lebendige ist zwar in Elemente zerlegt, aber man kann es aus diesen nicht wieder zusammenstellen und beleben"; the dictum of the *Cellularpathologie* being just the opposite, "Jedes Thier erscheint als eine Summe vitaler Einheiten, von denen jede den vollen Charakter des Lebens an sich trägt."

Hofmeister and Sachs have taught us that in the plant the growth

* *Theory of Cells*, p. 191.

† *The Cell in Development*, etc., p. 59; cf. 3rd ed. (1925), p. 102.

‡ E.g. Brücke, *Elementarorganismen*, p. 387: "Wir müssen in der Zelle einen kleinen Thierleib sehen, und dürfen die Analogien, welche zwischen ihr und den kleinsten Thierformen existiren, niemals aus den Augen lassen."

§ C. O. Whitman, The inadequacy of the cell-theory, *Journ. Morphol.* VIII, pp. 639-658, 1893; A. Sedgwick, On the inadequacy of the cellular theory of development, *Q.J.M.S.* XXXVII, pp. 87-101, 1895; XXXVIII, pp. 331-337, 1896. Cf. G. C. Bourne, *ibid.* XXXVIII, pp. 137-174, 1896; Clifford Dobell, The principles of Protistology, *Arch. f. Protistenk.* XXIII, p. 270, 1911.

|| Cf. O. Hertwig, *Die Zelle und die Gewebe*, 1893, p. 1: "Die Zellen, in welche der Anatom die pflanzlichen und thierischen Organismen zerlegt, sind die Träger der Lebensfunktionen; sie sind, wie Virchow sich ausgedrückt hat, die 'Lebenseinheiten.' Von diesem Gesichtspunkt aus betrachtet, erscheint der Gesamttriebprozess eines zusammengesetzten Organismus nichts Anderes zu sein als das höchst verwickelte Resultat der einzelnen Lebensprozesse seiner zahlreichen, verschieden funktionirenden Zellen." But in 1920 Doncaster (*Cytology*, p. 1) declared that "the old idea of discrete and independent cells is almost abandoned," and that the word *cell* was coming to be used "rather as a convenient descriptive term than as denoting a fundamental concept of biology"; and James Gray (*Experimental Cytology*, p. 2) said, in 1931, that "we must be careful to avoid any tacit assumption that the cell is a natural, or even legitimate, unit of life and function."

of the mass, the growth of the organ, is the primary fact, that "cell formation is a phenomenon very general in organic life, but still only of secondary significance." "Comparative embryology," says Whitman, "reminds us at every turn that the organism dominates cell-formation, using for the same purpose one, several, or many cells, massing its material and directing its movements and shaping its organs, as if cells did not exist*." So Rauber declared that, in the whole world of organisms, "das Ganze liefert die Theile, nicht die Theile das Ganze: letzteres setzt die Theile zusammen, nicht diese jenes†." And on the botanical side De Bary has summed up the matter in an aphorism, "Die Pflanze bildet Zellen, nicht die Zelle bildet Pflanzen."

Discussed almost wholly from the concrete, or morphological point of view, the question has for the most part been made to turn on whether actual protoplasmic continuity can be demonstrated between one cell and another, whether the organism be an actual reticulum, or syncytium‡. But from the dynamical point of view the question is much simpler. We then deal not with material continuity, not with little bridges of connecting protoplasm, but with a continuity of forces, a comprehensive field of force, which runs through and through the entire organism and is by no means restricted in its passage to a protoplasmic continuum. And such a continuous field of force, somehow shaping the whole organism, independently of the number, magnitude and form of the individual cells, which enter like a froth into its fabric, seems to me certainly and obviously to exist. As Whitman says, "the fact that physiological unity is not broken by cell-boundaries is confirmed in so many ways that it must be accepted as one of the fundamental truths of biology§."

* *Journ. Morph.* VIII, p. 653, 1893.

† *Neue Grundlegungen zur Kenntniss der Zelle, Morph. Jahrb.* VIII, pp. 272, 313, 333, 1883.

‡ Cf. e.g. Ch. van Bambeke, *A propos de la délimitation cellulaire, Bull. Soc. belge de Microsc.* XXIII, pp. 72-87, 1897.

§ *Journ. Morph.* II, p. 49, 1889.

CHAPTER V

THE FORMS OF CELLS

PROTOPLASM, as we have already said, is a fluid* or a semi-fluid substance, and we need not try to describe the particular properties of the colloid or jelly-like substances to which it is allied, or rather the characteristics of the “colloidal state” in which it and they exist; we should find it no easy matter†. Nor need we appeal to precise theoretical definitions of fluidity, lest we come into a debatable land. It is in the most general sense that protoplasm is “fluid.” As Graham said (of colloid matter in general), “its softness *partakes of fluidity*, and enables the colloid to become a vehicle for liquid diffusion, like water itself‡.” When we can deal with protoplasm in sufficient quantity we see it *flow*§; particles move freely through it, air-bubbles and liquid droplets shew round or spherical within it; and we shall have much to say about other phenomena manifested by its own surface, which are those especially characteristic of liquids. It may encompass and contain solid bodies, and it may “secrete” solid substances within or around itself; and it often happens in the complex living organism that these solid substances, such as shell or nail or horn or feather, remain when the protoplasm which formed them is dead and gone. But the protoplasm itself is fluid or semi-fluid, and permits of free (though not necessarily rapid) *diffusion* and easy *convection* of particles within itself, which simple fact is of elementary importance

* Cf. W. Kühne, *Ueber das Protoplasma*, 1864.

† Sand, or a heap of millet-seed, may in a sense be deemed a “fluid,” and such the learned Father Boscovich held them to be (*Theoria*, p. 427), but at best they are fluids without a surface. Galileo had drawn the same comparison; but went on to contrast the continuity, or infinite subdivision, of a fluid with the finite, discontinuous subdivision of a fine powder. Cf. Boyer, *Concepts of the Calculus*, 1939, p. 291.

‡ *Phil. Trans.* CLI, p. 183, 1861; *Researches*, ed. Angus Smith, 1877, p. 553. We no longer speak, however, of “colloids” in a specific sense, as Graham did; for any substance can be brought into the “colloidal state” by appropriate means or in an appropriate medium.

§ The copious protoplasm of a Myxomycete has been passed unharmed through filter-paper with a pore-size of about $1\ \mu$, or 0.001 mm.

in connection with form, throwing light on what seem to be common characteristics and peculiarities of the forms of living things.

Much has been done, and more said, about the nature of protoplasm since this book was written. Calling *cytoplasm* the cell-protoplasm after deduction of chloroplasts and other gross inclusions, we find it to contain fats, proteins, lecithin and some other substances combined with much water (up to 97 per cent.) to form a sort of watery *gel*. The microscopic structures attributed to it, alveolar, granular or fibrillar, are inconstant or invalid; but it does appear to possess an invisible or submicroscopic structure, distinguishing it from an ordinary colloid gel, and forming a quasi-solid framework or reticulum. This framework is based on proteid macromolecules, in the form of polypeptide chains, of great length and carrying in side-chains other organic constituents of the cytoplasm*. The polymerised units represent the *micellæ*† which the genius of Nägeli predicted or postulated more than sixty years ago; and we may speak of a "micellar framework" as representing in our cytoplasm the dispersed phase of an ordinary colloid. In short, as the cytoplasm is neither true fluid nor true solid, neither is it true colloid in the ordinary sense. Its micellar structure gives it a certain rigidity or tendency to retain its shape, a certain plasticity and tensile strength, a certain ductility or capacity to be drawn out in threads; but yet leaves it with a permeability (or semi-permeability), a capacity to swell by imbibition, above all an ability to stream and flow, which justify our calling it "fluid or semi-fluid," and account for its exhibition of surface-tension and other capillary phenomena.

The older naturalists, in discussing the differences between organic and inorganic bodies, laid stress upon the circumstance that the latter grow by "agglutination," and the former by what they termed "intussusception." The contrast is true; but it applies rather to solid or crystalline bodies as compared with colloids of all kinds, whether living or dead. But it so happens that the great majority of colloids are of organic origin; and out of them our bodies, and our food, and the very clothes we wear, are almost wholly made.

A crystal "grows" by deposition of new molecules, one by one and layer by layer, each one superimposed on the solid substratum

* See (*int. al.*) A. Frey-Wyssling, *Submikroskopische Morphologie des Protoplasmas*, Berlin, 1938; cf. *Nature*, June 10, 1939, p. 965; also A. R. Moore, in *Scientia*, LXII, July 1, 1937. On the nature of viscid fluid threads, cf. Larmor, *Nature*, July 11, 1936, p. 74.

† *Micella*, or *micula*, diminutive of *mīca*, a crumb, grain or morsel—*mīca panis, salis, turis*, etc. Nägeli used the word to mean an aggregation of molecules, as the molecule is an aggregation of atoms; the one, however, is a physical and the other a chemical concept. Roughly speaking, we may think of micellæ as varying from about 1 to 200 $\mu\mu$; they play a corresponding part in the "disperse phase" of a colloid to that played by the molecules in an ordinary solution. The macromolecules of modern chemistry are sometimes distinguished from these as still larger aggregates. See Carl Nägeli, *Das Mikroskop* (2nd ed.), 1877; *Theorie der Gahrung*, 1879.

already formed. Each particle would seem to be influenced only by the particles in its immediate neighbourhood, and to be in a state of freedom and independence from the influence, either direct or indirect, of its remoter neighbours. So Lavoisier was the first to say. And as Kelvin and others later on explained the formation and the resulting forms of crystals, so we believe that each added particle takes up its position in relation to its immediate neighbours already arranged, in the holes and corners that their arrangement leaves, and in closest contact with the greatest number*; hence we may repeat or imitate this process of arrangement, with great or apparently even with precise accuracy (in the case of the simpler crystalline systems), by piling up spherical pills or grains of shot. In so doing, we must have regard to the fact that each particle must drop into the place where it can go most easily, or where no easier place offers. In more technical language, each particle is free to take up, and does take up, its position of least potential energy relative to those already there: in other words, for each particle motion is induced until the energy of the system is so distributed that no tendency or resultant force remains to move it more. This has been shewn to lead to the production of *plane* surfaces† (in all cases where, by the limitation of material, surfaces *must* occur); where we have planes, there straight edges and solid angles must obviously occur also, and, if equilibrium is to follow, must occur symmetrically. Our piling up of shot to make mimic crystals gives us visible demonstration that the result is actually to obtain, as in the natural crystal, plane surfaces and sharp angles symmetrically disposed.

* Cf. Kelvin, On the molecular tactics of a crystal, *The Boyle Lecture*, Oxford, 1893; *Baltimore Lectures*, 1904, pp. 612–642. Here Kelvin was mainly following Bravais's (and Frankenheim's) theory of "space-lattices," but he had been largely anticipated by the crystallographers. For an account of the development of the subject in modern crystallography, by Sohncke, von Fedorow, Schönfliess, Barlow and others, see (e.g.) Tutton's *Crystallography*, and the many papers by W. E. Bragg and others.

† In a homogeneous crystalline arrangement, *symmetry* compels a locus of one property to be a plane or set of planes; the locus in this case being that of least surface potential energy. Crystals "seem to be, as it were, the Elemental Figures, or the A B C of Nature's working, the reason of whose curious Geometrical Forms (if I may so call them) is very easily explicable" (*Robert Hooke, Posthumous Works*, 1745, p. 280).

But the living cell grows in a totally different way, very much as a piece of glue swells up in water, by "imbibition," or by inter-penetration into and throughout its entire substance. The semi-fluid colloid mass takes up water, partly to combine chemically with its individual molecules*; partly by physical diffusion into the interstices between molecules or micellae, and partly, as it would seem, in other ways; so that the entire phenomenon is a complex and even an obscure one†. But, so far as we are concerned, the net result is very simple. For the equilibrium, or tendency to equilibrium, of fluid pressure in all parts of its interior while the process of imbibition is going on, the constant rearrangement of its fluid mass, the contrast in short with the crystalline method of growth where each particle comes to rest to move (relatively to the whole) no more, lead the mass of jelly to swell up very much as a bladder into which we blow air, and so, by a *graded* and harmonious distribution of forces, to assume everywhere a rounded and more or less bubble-like external form‡. So, when the same school of older naturalists called attention to a new distinction or contrast of form between organic and inorganic objects, in that the contours of the former tended to roundness and curvature, and those of the latter to be bounded by straight lines, planes and sharp angles, we see that this contrast was not a new and different one, but only another aspect of their former statement, and an immediate consequence of the difference between the processes of agglutination and intussusception§.

So far then as growth goes on undisturbed by pressure or other external force, the fluidity of the protoplasm, its mobility internal

* This is what Graham called the *water of gelatination*, on the analogy of *water of crystallisation*; *Chem. and Phys. Researches*, p. 597.

† On this important phenomenon, see J. R. Katz, *Gesetze der Quellung*, Dresden, 1916. Swelling is due to "concentrated solution," and is accompanied by increase of volume and liberation of energy, as when the Egyptians split granite by the swelling of wood.

‡ Here, in a non-crystalline or random arrangement of particles, symmetry ensures that the potential energy shall be the same per unit area of all surfaces; and it follows from geometrical considerations that the total surface energy will be least if the surface be spherical.

§ Intussusception has its shades of meaning; it is excluded from the idea of a crystalline body, but not limited to the ordinary conception of a colloid one. When new micellar strands become interwoven in the micro-structure of a cellulose cell-wall, that is a special kind of "intussusception."

and external*, and the way in which particles move freely hither and thither within, all manifestly tend to the production of swelling, rounded surfaces, and to their great predominance over plane surfaces in the contours of the organism. These rounded contours will tend to be preserved for a while, in the case of naked protoplasm by its viscosity, and in presence of a cell-wall by its very lack of fluidity. In a general way, the presence of curved boundary surfaces will be especially obvious in the unicellular organisms, and generally in the external form of all organisms, and wherever mutual pressure between adjacent cells, or other adjacent parts, has not come into play to flatten the rounded surfaces into planes.

The swelling of any object, organic or inorganic, living or dead, is bound to be influenced by any lack of structural symmetry or homogeneity†. We may take it that all elongated structures, such as hairs, fibres of silk or cotton, fibrillae of tendon and connective tissue, have by virtue of their elongation an invisible as well as a visible polarity. Moreover, the ultimate fibrils are apt to be invested by a protein different from the "collagen" within, and liable to swell more or to swell less. In ordinary tendons there is a "reticular sheath," which swells less, and is apt to burst under pressure from within; it breaks into short lengths, and when the strain is relieved these roll back, and form the familiar *annuli*. Another instance is the tendency to swell of the "macro-molecules" of many polymerised organic bodies, proteins among them.

But the rounded contours which are assumed and exhibited by a piece of hard glue when we throw it into water and see it expand as it sucks the water up, are not near so regular nor so beautiful as are those which appear when we blow a bubble, or form a drop, or even pour water into an elastic bag. For these curving contours depend upon the properties of the bag itself, of the film or membrane, which contains the mobile gas, or which contains or bounds the mobile liquid mass. And hereby, in the case of the fluid or semifluid mass, we are introduced to the subject of *surface-tension*: of which indeed we have spoken in the preceding chapter, but which we must now examine with greater care.

* The protoplasm of a sea-urchin's egg has a viscosity only about four times, and that of various plants not more than ten to twenty times, that of water itself. See, for a general discussion, L. V. Heilbrunn, *Colloid Symposium Monograph*, 1928.

† D. Jordan Lloyd and R. H. Marriott, The swelling of structural proteins, *Proc. R.S. (B)*, No. 810, pp. 439–445, 1935.

Among the forces which determine the forms of cells, whether they be solitary or arranged in contact with one another, this force of surface-tension is certainly of great, and is probably of paramount, importance. But while we shall try to separate out the phenomena which are directly due to it, we must not forget that, in each particular case, the actual conformation which we study may be, and usually is, the more or less complex resultant of surface-tension acting together with gravity, mechanical pressure, osmosis, or other physical forces. The peculiar beauty of a soap-bubble, solitary or in collocation, depends on the absence (to all intents and purposes) of these alien forces from the field; hence Plateau spoke of the films which were the subject of his experiments as "*lames fluides sans pesanteur.*" The resulting form is in such a case so pure and simple that we come to look on it as wellnigh a mathematical abstraction.

Surface-tension, then, is that force by which we explain the form of a drop or of a bubble, of the surfaces external and internal of a "froth" or collocation of bubbles, and of many other things of like nature and in like circumstances*. It is a property of liquids (in the sense at least with which our subject is concerned), and it is manifested at or very near the surface, where the liquid comes into contact with another liquid, a solid or a gas. We note here that the term *surface* is to be interpreted in a wide sense; for wherever we have solid particles embedded in a fluid, wherever we have a non-homogeneous fluid or semi-fluid, or a "two-phase colloid" such as a particle of protoplasm, wherever we have the presence of "impurities" as in a mass of molten metal, there we have always to bear in mind the existence of *surfaces* and of surface-phenomena, not only on the exterior of the mass but also throughout its interstices, wherever like and unlike meet.

* The idea of a "surface-tension" in liquids was first enunciated by Segner, and ascribed by him to forces of attraction whose range of action was so small "ut nullo adhuc sensu percipi potuerat" (*De figuris superficierum fluidarum*, in *Comment. Soc. Roy. Göttingen*, 1751, p. 301). Hooke, in the *Micrographia* (1665, Obs. VIII, etc.), had called attention to the globular or spherical form of the little morsels of steel struck off by a flint, and had shewn how to make a powder of such spherical grains, by heating fine filings to melting point. "This Phaenomenon" he said "proceeds from a propriety which belongs to all kinds of fluid Bodies more or less, and is caused by the Incongruity of the Ambient and included Fluid, which so acts and modulates each other, that they acquire, as neer as is possible, a *spherical* or *globular* form...."

A liquid in the mass is devoid of structure; it is homogeneous, and without direction or polarity. But the very concept of surface-tension forbids this to be true of the surface-layer of a body of liquid, or of the "interphase" between two liquids, or of any film, bubble, drop, or capillary jet or stream. In all these cases, and more emphatically in the case of a "monolayer," even the liquid has a structure of its own; and we are reminded once again of how largely the living organism, whether high or low, is composed of colloid matter in precisely such forms and structural conditions.

Surface-tension is due to molecular force*: to force, that is to say, arising from the action of one molecule upon another; and since we can only ascribe a small "sphere of action" to each several molecule, this force is manifested only within a narrow range. Within the interior of the liquid mass we imagine that such molecular interactions negative one another; but at and near the free surface, within a layer or film approximately equal to the range of the molecular force—or to the radius of the aforesaid "sphere of action"—there is a lack of equilibrium and a consequent manifestation of force.

The action of the molecular forces has been variously explained. But one simple explanation (or mode of statement) is that the molecules of the surface-layer are being constantly attracted into the interior by such as are just a little more deeply situated; the surface shrinks as molecules keep quitting it for the interior, and this *surface-shrinkage* exhibits itself as a *surface-tension*. The process continues till it can go no farther, that is to say until the surface itself becomes a "minimal area†." This is a sufficient description of the phenomenon in cases where a portion of liquid is subject to no other than its own molecular forces, and (since the sphere has,

* While we *explain* certain phenomena of the organism by reference to atomic or molecular forces, the following words of Du Bois Reymond's seem worth recalling: "Naturerkennen ist Zurückführen der Veränderungen in der Körperwelt auf Bewegung von Atomen, die durch deren von der Zeit unabhängige Centralkräfte bewirkt werden, oder Auflösung der Naturkräfte in Mechanik der Atome. Es ist eine psychologische Erfahrungstatsache dass, wo solche Auflösung gelängt, unser Causalbedürfniss vorläufig sich befriedigt fühlt" (*Ueber die Grenzen des Naturerkennens*, Leipzig, 1873).

† There must obviously be a certain kinetic energy in the molecules within the drop, to balance the forces which are trying to contract and diminish the surface.

of all solids, the least surface for a given volume) it accounts for the spherical form of the raindrop*, of the grain of shot, or of the living cell in innumerable simple organisms†. It accounts also, as we shall presently see, for many much more complicated forms, manifested under less simple conditions.

Let us note in passing that surface-tension is a comparatively small force and is easily measurable: for instance that between water and air is equivalent to but a few grains per linear inch, or a few grammes per metre. But this small tension, when it exists in a *curved* surface of great curvature, such as that of a minute drop, gives rise to a very great pressure, directed inwards towards the centre of curvature. We may easily calculate this pressure, and so satisfy ourselves that, when the radius of curvature approaches molecular dimensions, the pressure is of the order of thousands of atmospheres—a conclusion which is supported by other physical considerations.

The contraction of a liquid surface, and the other phenomena of surface-tension, involve the doing of work, and the power to do work is what we call Energy. The whole energy of the system is diffused throughout its molecules, as is obvious in such a simple case as we have just considered; but of the whole stock of energy only the part residing at or very near the surface normally manifests itself in work, and hence we speak (though the term be open to

* Raindrops must be spherical, or they would not produce a rainbow; and the fact that the upper part of the bow is the brightest and sharpest shews that the higher raindrops are more truly spherical, as well as smaller than the lower ones. So also the smallest dewdrops are found to be more iridescent than the large, shewing that they also are the more truly spherical; cf. T. W. Backhouse, in *Monthly Meteorol. Mag.* March, 1879. Mercury has a high surface-tension, and its globules are very nearly round.

† That the offspring of a spherical cell (whether it be raindrop, plant or animal) should be also a spherical cell, would seem to need no other explanation than that both are of identical substance, and each subject to a similar equilibrium of surface-forces; but the biologists have been apt to look for a subtler reason. Giglio-Tos, speaking of a sea-urchin's dividing egg, asks why the daughter-cells are spherical like the mother-cell, and finds the reason in "heredity": "Wenn also die letztere (d. i. die Mutterzelle) eine sphärische Form besass, so nehmen auch die Töchterzellen dieselbe ein; wäre ursprünglich eine kubische Form vorhanden, so würden also auch die Töchterzellen dieselbe auch aneignen. Die Ursache warum die Töchterzellen die sphärische Form anzunehmen trachten liegt darin, dass diese die Ur- und Grundform aller Zellen ist, sowohl bei Tieren wie bei den Pflanzen" (*Arch. f. Entw. Mech.* LI, p. 115, 1922).

some objection) of a specific *surface-energy*. Surface-energy, and the way it is increased and multiplied by the multiplication of surfaces due to the subdivision of the tissues into cells, is of the highest interest to the physiologist; and even the morphologist cannot pass it by. For the one finds surface-energy present, often perhaps paramount, in every cell of the body; and the other may find, if he will only look for it, the form of every solitary cell, like that of any other drop or bubble, related to if not controlled by capillarity. The theory of "capillarity," or "surface-energy," has been set forth with the utmost possible lucidity by Tait and by Clerk Maxwell, on whom the following paragraphs are based: they having based their teaching on that of Gauss*, who rested on Laplace.

Let E be the whole potential energy of a mass M of liquid; let e_0 be the energy per unit mass of the interior liquid (we may call it the *internal energy*); and let e be the energy per unit mass for a layer of the skin, of surface S , of thickness t , and density ρ (e being what we call the *surface-energy*). It is obvious that the total energy consists of the internal *plus* the surface-energy, and that the former is distributed through the whole mass, minus its surface layers. That is to say, in mathematical language,

$$E = (M - S, \Sigma t\rho) e_0 + S \cdot \Sigma t\rho e.$$

But this is equivalent to writing:

$$= M e_0 + S \cdot \Sigma t\rho (e - e_0);$$

and this is as much as to say that the total energy of the system may be taken to consist of two portions, one uniform throughout the whole mass, and another, which is proportional on the one hand to the amount of surface, and on the other hand to the difference between e and e_0 , that is to say to the difference between the unit values of the internal and the surface energy.

It was Gauss who first shewed how, from the mutual attractions between all the particles, we are led to an expression for what we

* See Gauss's *Principia generalia Theoriae Figurae Fluidorum in statu equilibrii*, Göttingen, 1830. The historical student will not overlook the claims to priority of Thomas Young, in his Essay on the cohesion of fluids, *Phil. Trans.* 1805; see the account given in his *Life* by Dean Peacock, 1855, pp. 199–210.

now call the *potential energy** of the system; and we know, as a fundamental theorem of dynamics, as well as of molecular physics, that the potential energy of the system tends to a minimum, and finds in that minimum its stable equilibrium.

We see in our last equation that the term Me_0 is irreducible, save by a reduction of the mass itself. But the other term may be diminished (1) by a reduction in the area of surface, S , or (2) by a tendency towards equality of e and e_0 , that is to say by a diminution of the specific surface energy, e .

These then are the two methods by which the energy of the system will manifest itself in work. The one, which is much the more important for our purposes, leads always to a diminution of surface, to the so-called "principle of minimal areas"; the other, which leads to the lowering (under certain circumstances) of surface tension, is the basis of the theory of Adsorption, to which we shall have some occasion to refer as the *modus operandi* in the development of a cell-wall, and in a variety of other histological phenomena. In the technical phraseology of the day, the "capacity factor" is involved in the one case, and the "intensity factor" in the other†.

Inasmuch as we are concerned with the *form* of the cell, it is the former which becomes our main postulate: telling us that the energy-equations of the surface of a cell, or of the free surfaces of cells in partial contact, or of the partition-surfaces of cells in contact with one another, all indicate a minimum of potential energy in the system, by which minimal condition the system is brought, *ipso facto*, into equilibrium. And we shall not fail to observe, with something more than mere historical interest and curiosity, how

* The word *Energy* was substituted for the old *vis viva* by Thomas Young early in the nineteenth century, and was used by James Thomson, Lord Kelvin's brother, about 1852, to mean, more generally, "capacity for doing work." The term *potential*, or *latent*, in contrast to *actual* energy, in other words the distinction between "energy of activity and energy of configuration," was proposed by Macquorn Rankine, and suggested to him by Aristotle's use of *δύναμις* and *ένέργεια*; see Rankine's paper On the general law of the transformation of energy, *Phil. Soc. Glasgow*, Jan. 5, 1853, cf. *ibid.* Jan. 23, 1867, and *Phil. Mag.* (4), xxvii, p. 404, 1864. The phrase *potential energy* was at once adopted, but *kinetic* was substituted for *actual* by Thomson and Tait.

† The capacity factor, inasmuch as it leads to diminution of surface, is responsible for the concrescence of droplets into drops, of microcrystals into larger units, for the flocculation of colloids, and for many other similar "changes of state."

deeply and intrinsically there enter into this whole class of problems the method of maxima and minima discovered by Fermat, the "loi universelle de repos" of Maupertuis, "dont tous les cas d'équilibre dans la statique ordinaire ne sont que des cas particuliers", and the *lineae curvae maximi minimive proprietatibus gaudentes* of Euler, by which principles these old natural philosophers explained correctly a multitude of phenomena, and drew the lines whereon the foundations of great part of modern physics are well and truly laid. For that physical laws deal with *minima* is very generally true, and is highly characteristic of them. The hanging chain so hangs that the height of its centre of gravity is a minimum; a ray of light takes the path, however devious, by which the time of its journey is a minimum; two chemical substances in reaction so behave that their thermodynamic potential tends to a minimum, and so on. The natural philosophers of the eighteenth century were engrossed in minimal problems; and the differential equations which solve them nowadays are among the most useful and most characteristic equations in mathematical physics.

"Voici," said Maupertuis, "dans un assez petit volume à quoi je reduis mes ouvrages mathématiques!" And when Lagrange, following Euler's lead*, conceived the principle of least action, he regarded it not as a metaphysical principle but as "un résultat simple et général des lois de la mécanique†." The principle of least action‡ explains nothing, it tells us nothing of causation, yet it illuminates a host of things. Like Maxwell's equations and other such flashes of genius it clarifies our knowledge, adds weight to our observations, brings order into our stock-in-trade of facts. It embodies and extends that "law of simplicity" which Borelli was the first to lay down: "Lex perpetua Naturae est ut agat minimo labore, mediis et modis simplicissimis, facillimis, certis et

* Euler, *Traité des Isopérimètres*, Lausanne, 1744.

† Lagrange, *Mécanique Analytique* (2), II, p. 188; ed. in 4to, 1788.

‡ This profound conception, not less metaphysical in the outset than physical, began in the seventeenth century with Fermat, who shewed (in 1629) that a ray of light followed the quickest path available, or, as Leibniz put it, *via omnium facillima*; it was over this principle that Voltaire quarrelled with Euler and Maupertuis. The mathematician will think also of Hamilton's restatement of the principle, and of its extension to the theory of probabilities by Boltzmann and Willard Gibbs. Cf. (*int. al.*) A. Mayer, *Geschichte des Prinzips der kleinsten Action*, 1877.

tutis: evitando, quam maxime fieri potest, incommoditates et prolixitates." The principle of least action grew up, and grew quickly, out of cruder, narrower notions of "least time" or "least space or distance." Nowadays it is developing into a principle of "least action in space-time," which shall still govern and predict the motions of the universe. The infinite perfection of Nature is expressed and reflected in these concepts, and Aristotle's great aphorism that "Nature does nothing in vain" lies at the bottom of them all.

In all cases where the principle of maxima and minima comes into play, as it conspicuously does in films at rest under surface-tension, the configurations so produced are characterised by obvious and remarkable *symmetry**. Such symmetry is highly characteristic of organic forms, and is rarely absent in living things—save in such few cases as *Amoeba*, where the rest and equilibrium on which symmetry depends are likewise lacking. And if we ask what physical equilibrium has to do with formal symmetry and structural regularity, the reason is not far to seek, nor can it be better put than in these words of Mach's†: "In every symmetrical system every deformation that tends to destroy the symmetry is complemented by an equal and opposite deformation that tends to restore it. In each deformation, positive and negative work is done. One condition, therefore, though not an absolutely sufficient one, that a maximum or minimum of work corresponds to the form of equilibrium, is thus supplied by symmetry. Regularity is successive symmetry; there is no reason, therefore, to be astonished that the forms of equilibrium are often symmetrical and regular."

A crystal is the perfection of symmetry and of regularity; symmetry is displayed in its external form, and regularity revealed in its internal lattices. Complex and obscure as the attractions, rotations, vibrations and what not within the crystal may be, we rest assured that the configuration, repeated again and again, of

* On the mathematical side, cf. Jacob Steiner, *Einfache Beweise der isoperimetrischen Hauptsätze*, *Abh. k. Akad. Wiss. Berlin*, xxiii, pp. 116–135, 1836 (1838). On the biological side, see (*int. al.*) F. M. Jaeger, *Lectures on the Principle of Symmetry, and its application to the natural sciences*, Amsterdam, 1917; also F. T. Lewis, *Symmetry... in evolution*, *Amer. Nat.* lvii, pp. 5–41, 1923.

† *Science of Mechanics*, 1902, p. 395; see also Mach's article *Ueber die physikalische Bedeutung der Gesetze der Symmetrie*, *Lotos*, xxi, pp. 139–147, 1871.

the component atoms is precisely that for which the energy is a minimum; and we recognise that this minimal distribution is of itself tantamount to symmetry and to stability.

Moreover, the principle of least action is but a setting of a still more universal law—that the world and all the parts thereof tend ever to pass from less to more probable configurations; in which the physicist recognises the principle of Clausius, or second law of thermodynamics, and with which the biologist must somehow reconcile the whole “theory of evolution.”

As we proceed in our enquiry, and especially when we approach the subject of *tissues*, or agglomerations of cells, we shall have from time to time to call in the help of elementary mathematics. But already, with very little mathematical help, we find ourselves in a position to deal with some simple examples of organic forms.

When we melt a stick of sealing-wax in the flame, surface-tension (which was ineffectively present in the solid but finds play in the now fluid mass) rounds off its sharp edges into curves, so striving towards a surface of minimal area; and in like manner, by merely melting the tip of a thin rod of glass, Hooke made the little spherical beads which served him for a microscope*. When any drop of protoplasm, either over all its surface or at some free end, as at the extremity of the pseudopodium of an amoeba, is seen likewise to “round itself off,” that is not an effect of “vital contractility,” but, as Hofmeister shewed so long ago as 1867, a simple consequence of surface-tension; and almost immediately afterwards Engelmann† argued on the same lines, that the forces which cause the contraction of protoplasm in general may “be just the same as those which tend to make every non-spherical drop of fluid become spherical.” We are not concerned here with the many theories and speculations which would connect the phenomena of surface-tension with contractility, muscular movement, or other special *physiological* func-

* Similarly, Sir David Brewster and others made powerful lenses by simply dropping small drops of Canada balsam, castor oil, or other strongly refractive liquids, on to a glass plate: *On New Philosophical Instruments* (Description of a new fluid microscope), Edinburgh, 1813, p. 413. See also Hooke's *Micrographia*, 1665; and Adam's *Essay on the Microscope*, 1798, p. 8: “No person has carried the use of these globules so far as Father Torre of Naples, etc.” Leeuwenhoek, on the other hand, *ground* his lenses with exquisite skill.

† Beiträge zur Physiologie des Protoplasma, *Pflüger's Archiv*, II, p. 307, 1869.

tions, but we find ample room to trace the operation of the same cause in producing, under conditions of rest and equilibrium, certain definite and inevitable forms.

It is of great importance to observe that the living cell is one of those cases where the phenomena of surface-tension are by no means limited to the *outer* surface; for within the heterogeneous emulsion of the cell, between the protoplasm and its nuclear and other contents, and in the "alveolar network" of the cytoplasm itself (so far as that alveolar structure is actually present in life), we have a multitude of interior surfaces; and, especially among plants, we may have large internal "interfacial contacts" between the protoplasm and its included granules, or its vacuoles filled with the "cell-sap." Here we have a great field for surface-action; and so long ago as 1865, Nägeli and Schwendener shewed that the streaming currents of plant cells might be plausibly explained by this phenomenon. Even ten years earlier, Weber had remarked upon the resemblance between the protoplasmic streamings and the currents to be observed in certain inanimate drops for which no cause but capillarity could be assigned*. What sort of chemical changes lead up to, or go hand in hand with, the variations of surface-tension in a living cell, is a vastly important question. It is hardly one for us to deal with; but this at least is clear, that the phenomenon is more complicated than its first investigators, such as Bütschli and Quincke, ever took it to be. For the lowered surface-tension which leads, say, to the throwing out of a pseudopodium, is accompanied first by local acidity, then by local adsorption of proteins, lastly and consequently by gelation; and this last is tantamount to the formation of "ectoplasm"—a step in the direction of encystment†.

The elementary case of *Amoeba* is none the less a complicated one. The "amoeboid" form is the very negation of rest or of equilibrium;

* Poggendorff's *Annalen*. xciv, pp. 447–459, 1855. Cf. Strethill Wright, *Phil. Mag.* Feb. 1860; *Journ. Anat. and Physiol.* i, p. 337, 1867.

† Cf. C. J. Pantin, *Journ. Mar. Biol. Assoc.* xiii, p. 24, 1923; *Journ. Exp. Biol.* 1923 and 1926; S. O. Mast, *Journ. Morph.* xli, p. 347, 1926; and O. W. Tiegs, Surface tension and the theory of protoplasmic movement, *Protoplasma*, iv, pp. 88–139, 1928. See also (*int. al.*) N. K. Adam, *Physics and Chemistry of Surfaces*, 1930; also Discussion on colloid science applied to biology (*passim*), *Trans. Faraday Soc.* xxvi, pp. 663 seq., 1930.

the creature is always moving, from one protean configuration to another; its surface-tension is never constant, but continually varies from here to there. Where the surface tension is greater, that portion of the surface will contract into spherical or spheroidal forms; where it is less, the surface will correspondingly extend. While generally speaking the surface-energy has a minimal value, it is not necessarily constant. It may be diminished by a rise of temperature; it may be altered by contact with adjacent substances*, by the transport of constituent materials from the interior to the surface, or again by actual chemical and fermentative change; for within the cell, the surface-energies developed about its heterogeneous contents will continually vary as these contents are affected by chemical metabolism. As the colloid materials are broken down and as the particles in suspension are diminished in size the "free surface-energy" will be increased, but the osmotic energy will be diminished†. Thus arise the various fluctuations of surface-tension, and the various phenomena of amoeboid form and motion, which Bütschli and others have reproduced or imitated by means of the fine emulsions which constitute their "artificial amoebae."

A multitude of experiments shew how extraordinarily delicate is the adjustment of the surface-tension forces, and how sensitive they are to the least change of temperature or chemical state. Thus,

* Haycraft and Carlier pointed out long ago (*Proc. R.S.E.* xv, pp. 220–224, 1888) that the amoeboid movements of a white blood-corpuscle are only manifested when the corpuscle is in contact with some solid substance: while floating freely in the plasma or serum of the blood, these corpuscles are spherical, that is to say they are at rest and in equilibrium. The same fact was recorded anew by Ledingham (On phagocytosis from an adsorptive point of view, *Journ. Hygiene*, xii, p. 324, 1912). On the emission of pseudopodia as brought about by changes in surface tension, see also (*int. al.*) J. A. Ryder, *Dynamics in Evolution*, 1894; Jensen, Ueber den Geotropismus niederer Organismen, *Pflüger's Archiv*, LIII, 1893. Jensen remarks that in Orbitolites, the pseudopodia issuing through the pores of the shell first float freely, then as they grow longer bend over till they touch the ground, whereupon they begin to display amoeboid and streaming motions. Verworn indicates (*Allg. Physiol.* 1895, p. 429), and Davenport says (*Exper. Morphology*, II, p. 376), that "this persistent clinging to the substratum is a 'thigmotropic' reaction, and one which belongs clearly to the category of 'response'." Cf. Pütter, Thigmotaxis bei Protisten, *Arch. f. Physiol.* 1900, Suppl. p. 247; but it is not clear to my mind that to account for this simple phenomenon we need invoke other factors than gravity and surface-action.

† Cf. Pauli, *Allgemeine physikalische Chemie d. Zellen u. Gewebe*, in Asher-Spiro's *Ergebnisse der Physiologie*, 1912; Przibram, *Vitalität*, 1913, p. 6.

on a plate which we have warmed at one side a drop of alcohol runs towards the warm area, a drop of oil away from it; and a drop of water on the glass plate exhibits lively movements when we bring into its neighbourhood a heated wire, or a glass rod dipped in ether*. The water-colour painter makes good use of the surface-tension effect of the minutest trace of ox-gall. When a plasmodium of *Aethalium* creeps towards a damp spot or a warm spot, or towards substances which happen to be nutritious, and creeps away from solutions of sugar or of salt, we are dealing with phenomena too often ascribed to 'purposeful' action or adaptation, but every one of which can be paralleled by ordinary phenomena of surface-tension†. The soap-bubble itself is never in equilibrium: for the simple reason that its film, like the protoplasm of *Amoeba* or *Aethalium*, is exceedingly heterogeneous. Its surface-energies vary from point to point, and chemical changes and changes of temperature increase and magnify the variation. The surface of the bubble is in continual movement, as more concentrated portions of the soapy fluid make their way outwards from the deeper layers; it thins and it thickens, its colours change, currents are set up in it and little bubbles glide over it; it continues in this state of restless movement as its parts strive one with another in their interactions towards unattainable equilibrium‡. On reaching a certain tenuity the bubble bursts: as is bound to happen when the attenuated film has no longer the properties of *matter in mass*.

* So Bernstein shewed that a drop of mercury in nitric acid moves towards, or is "attracted by," a crystal of potassium bichromate; *Pflüger's Archiv*, LXXX, p. 628, 1900.

† The surface-tension theory of protoplasmic movement has been denied by many. Cf. (e.g.) H. S. Jennings, Contributions to the behaviour of the lower organisms, *Carnegie Instit.* 1904, pp. 130–230; O. P. Dellinger, Locomotion of Amoebae, etc., *Journ. Exp. Zool.* III, pp. 337–357, 1906; also various papers by Max Heidenhain, in Merkels *Anatomische Hefte*; etc.

‡ These motions of a liquid surface, and other still more striking movements, such as those of a piece of camphor floating on water, were at one time ascribed by certain physicists to a peculiar force, *sui generis*, the *force épipolique* of Dutrochet: until van der Mensbrugghe shewed that differences of surface-tension were enough to account for this whole series of phenomena (*Sur la tension superficielle des liquides, considérée au point de vue de certains mouvements observés à leur surface, Mém. Cour. Acad. de Belgique*, XXXIV, 1869, *Phil. Mag.* Sept. 1867; cf. Plateau, *Statique des Liquides*, p. 283). An interesting early paper is by Dr G. Carradini of Pisa, Dell' adesione o attrazione di superficie, *Mem. di Matem. e di Fisica d. Soc. Ital. d. Sci. (Modena)*, XI, p. 75, XII, p. 89, 1804–5.

The film becomes a mere bimolecular, or even a monomolecular, layer; and at last we may treat it as a simple "surface of discontinuity." So long as the changes due to imperfect equilibrium are taking place *very slowly*, we speak of the bubble as "at rest"; it is then, as Willard Gibbs remarks, that the characters of a film are most striking and most sharply defined*.

So also, and surely not less than the soap-bubble, is every cell-surface a complex affair. Face and interface have a molecular orientation of their own, depending both on the partition-membrane and on the phases on either side. It is a variable orientation, changing at short intervals of space and time; it coincides with inconstant fields of force, electrical and other; it initiates, and controls or catalyses, chemical reactions of great variety and importance. In short we acknowledge and confess that, in simplifying the surface phenomena of the cell, for the time being and for our purely morphological ends, we may be losing sight, or making abstraction, of some of its most specific physical and physiological characteristics.

In the case of the naked protoplasmic cell, as the amoeboid phase is emphatically a phase of freedom and activity, of unstable equilibrium, of chemical and physiological change, so on the other hand does the spherical form indicate a phase of stability, of inactivity, of rest. In the one phase we see unequal surface-tensions manifested in the creeping movements of the amoeboid body, in the rounding-off of the ends of its pseudopodia, in the flowing out of its substance over a particle of "food," and in the current-motions in the interior of its mass; till, in the alternate phase, when internal homogeneity and equilibrium have been as far as possible attained and the potential energy of the system is at a minimum, the cell assumes a rounded or spherical form, passes into a state of "rest," and (for a reason which we shall presently consider) becomes at the same time encysted†.

* On the equilibrium of heterogeneous substances, *Collected Works*, 1, pp. 55-353; *Trans. Conn. Acad.* 1876-78.

† We still speak of the *naked protoplasm* of *Amoeba*; but short, and far short, of "encystment," there is always a certain tendency towards adsorptive action, leading to a surface-layer, or "plasma-membrane," still semi-fluid but less fluid than before, and different from the protoplasm within; it was one of the first and chief things revealed by the new technique of "micro-dissection." Little is known of

In their amoeboid phase the various Amoebae are just so many varying distributions of surface-energy, and varying amounts of surface-potential*. An ordinary floating drop is a figure of equilibrium under conditions of which we shall soon have something to say; and if both it and the fluid in which it floats be homogeneous it will be a round drop, a "figure of revolution." But the least chemical heterogeneity will cause the surface-tension to vary here and there, and the drop to change its form accordingly. The little swarm-spores of many algae lose their flagella as they settle down, and become mere drops of protoplasm for the time being; they "put out pseudopodia"—in other words their outline changes; and presently this amoeboid outline grows out into characteristic lobes or lappets, a sign of more or less symmetrical heterogeneity in the cell-substance.

In a budding yeast-cell (Fig. 103 A), we see a definite and restricted change of surface-tension. When a "bud" appears, whether with or without actual growth by osmosis or otherwise of the mass, it does so because at a certain part of the cell-surface the tension has diminished, and the area of that portion expands accordingly; but in turn the surface-tension of the expanded or extruded portion makes itself felt, and the bud rounds itself off into a more or less spherical form. The yeast-cell with its bud is a simple example of an important principle. Our whole treatment of cell-form in relation to surface-tension depends on the fact (which Errera was the first to give clear expression to) that the *incipient* cell-wall retains with but little impairment the properties of a liquid film†, and that the growing cell, in spite of the wall by which it has begun to be surrounded,



Fig. 103 A.

the physical nature of this so-called membrane. It behaves more or less like a fluid lipid envelope, immiscible with its surroundings. It is easily injured and easily repaired, and the well-being of the internal protoplasm is said to depend on the maintenance of its integrity. Robert Chambers, *Physical Properties of Protoplasm*, 1926; The living cell as revealed by microdissection, *Harvey Lectures*, Ser. XXII, 1926-27; *Journ. Gen. Physiol.* VIII, p. 369, 1926; etc.

* See (*int. al.*) Mary J. Hogue, The effect of media of different densities on the shape of Amoebae, *Journ. Exp. Zool.* XXII, pp. 565-572, 1917. Scheel had said in 1889 that *A. radiosa* is only an early stage of *A. proteus* (*Festschr. z. 70. Geburtsjg C. V. Kupffer*).

† Cf. *infra*, p. 561.

behaves very much like a fluid drop. So, to a first approximation, even the yeast-cell shews, by its ovoid and non-spherical form, that it has acquired its shape under some influence other than the uniform and symmetrical surface-tension which makes a soap-bubble into a sphere. This oval or any other asymmetrical form, once acquired, may be retained by virtue of the solidification and consequent rigidity of the membrane-like wall of the cell; and, unless rigidity ensue, it is plain that such a conformation as that of the yeast-cell with its attached bud could not be long retained as a figure of even partial equilibrium. But as a matter of fact, the cell in this case is not in equilibrium at all; it is *in process* of budding, and is slowly altering its shape by rounding off its bud. In like manner the developing egg, through all its successive phases of form, is never in complete equilibrium: but is constantly responding to slowly changing conditions, by phases of partial, transitory, unstable and conditional equilibrium.

There are innumerable solitary plant-cells, and unicellular organisms in general, which, like the yeast-cell, do not correspond to any of the simple forms which may be generated under the influence of simple and homogeneous surface-tension; and in many cases these forms, which we should expect to be unstable and transitory, have become fixed and stable by reason of some comparatively sudden solidification of the envelope. This is the case, for instance, in the more complicated forms of diatoms or of desmids, where we are dealing, in a less striking but even more curious way than in the budding yeast-cell, not with one simple act of formation, but with a complicated result of successive stages of localised growth, interrupted by phases of partial consolidation. The original cell has acquired a certain form, and then, under altering conditions and new distributions of energy, has thickened here or weakened there, and has grown out, or tended (as it were) to branch, at particular points. We can often trace in each particular stage of growth, or at each particular temporary growing point, the laws of surface tension manifesting themselves in what is for the time being a fluid surface; nay more, even in the adult and completed structure we have little difficulty in tracing and recognising (for instance in the outline of such a desmid as *Euastrum*) the rounded lobes which have successively grown or flowed out from the original rounded and

flattened cell. What we see in a many chambered foraminifer, such as *Globigerina* or *Rotalia*, is the same thing, save that the stages are more separate and distinct, and the whole is carried out to greater completeness and perfection. The little organism as a whole is not a figure of equilibrium nor of minimal area; but each new bud or separate chamber is such a figure, conditioned by the forces of surface-tension, and superposed upon the complex aggregate of similar bubbles after these latter have become consolidated one by one into a rigid system.

Let us now make some enquiry into the forms which a fluid surface can assume under the mere influence of surface-tension. In doing so we are limited to conditions under which other forces are relatively unimportant, that is to say where the surface energy is a considerable fraction of the whole energy of the system; and in general this will be the case when we are dealing with portions of liquid so small that their dimensions come within or near to what we have called the molecular range, or, more generally, in which the "specific surface" is large. In other words it is the small or minute organisms, or small cellular elements of larger organisms, whose forms will be governed by surface-tension; while the forms of the larger organisms are due to other and non-molecular forces. A large surface of water sets itself level because here gravity is predominant; but the surface of water in a narrow tube is curved, for the reason that we are here dealing with particles which lie within the range of each other's molecular forces. The like is the case with the cell-surfaces and cell-partitions which we are about to study, and the effect of gravity will be especially counteracted and concealed when the object is immersed in a liquid of nearly its own density.

We have already learned, as a fundamental law of "capillarity," that a liquid film *in equilibrium* assumes a form which gives it a minimal area under the conditions to which it is subject. These conditions include (1) the form of the boundary, if such exist, and (2) the pressure, if any, to which the film is subject: which pressure is closely related to the volume of air, or of liquid, that the film (if it be a closed one) may have to contain. In the simplest of cases, as when we take up a soap-film on a plane wire ring, the film is exposed to equal atmospheric pressure on both sides, and it ob-

viously has its minimal area in the form of a plane. So long as our wire ring lies in one plane (however irregular in outline), the film stretched across it will still be in a plane; but if we bend the ring so that it lies no longer in a plane, then our film will become curved into a surface which may be extremely complicated, but is still the smallest possible surface which can be drawn continuously across the uneven boundary.

The question of pressure involves not only external pressures acting on the film, but also that which the film itself is capable of exerting. For we have seen that the film is always contracting to the utmost; and when the film is curved, this leads to a pressure directed inwards—perpendicular, that is to say, to the surface of the film. In the case of the soap-bubble, the uniform contraction of whose surface has led to its spherical form, this pressure is balanced by the pressure of the air within; and if an outlet be given for this air, then the bubble contracts with perceptible force until it stretches across the mouth of the tube, for instance across the mouth of the pipe through which we have blown the bubble. A precisely similar pressure, directed inwards, is exercised by the surface layer of a drop of water or a globule of mercury, or by the surface pellicle on a portion or “drop” of protoplasm. Only we must always remember that in the soap-bubble, or the bubble which a glass-blower blows, there is a twofold pressure as compared with that which the surface-film exercises on the drop of liquid of which it is a part; for the bubble consists (unless it be so thin as to consist of a mere layer of molecules*) of a liquid layer, with a free surface within and another without, and each of these two surfaces exercises its own independent and coequal tension and its corresponding pressure†.

If we stretch a tape upon a flat table, whatever be the tension of the tape it obviously exercises no pressure upon the table below. But if we stretch it over a *curved* surface, a cylinder for instance, it does exercise a downward pressure; and the more curved the surface the greater is this pressure, that is to say the greater is this share of the entire force of tension which is resolved in the down-

* Or, more strictly speaking, unless its thickness be less than twice the range of the molecular forces.

† It follows that the tension of a bubble, depending only on the surface-conditions, is independent of the thickness of the film.

ward direction. In mathematical language, the pressure (p) varies directly as the tension (T), and inversely as the radius of curvature (R): that is to say, $p = T/R$, per unit of surface.

If instead of a cylinder, whose curvature lies only in one direction, we take a case of curvature in two dimensions (as for instance a sphere), then the effects of these two curvatures must be added together to give the resulting pressure p : which becomes equal to $T/R + T/R'$, or

$$p = \frac{1}{R} + \frac{1}{R'}.$$

And if in addition to the pressure p , which is due to surface-tension, we have to take into account other pressures, p' , p'' , etc., due to gravity or other forces, then we may say that the total pressure

$$P = p' + p'' + T \left(\frac{1}{R} + \frac{1}{R'} \right).$$

We may have to take account of the extraneous pressures in some cases, as when we come to speak of the shape of a bird's egg; but in this first part of our subject we are able for the most part to neglect them.

Our equation is an equation of equilibrium. The resistance to compression—the pressure outwards—of our fluid mass is a constant quantity (P); the pressure inwards, $T(1/R + 1/R')$, is also constant; and if the surface (unlike that of the mobile amoeba) be homogeneous, so that T is everywhere equal, it follows that $1/R + 1/R' = C$ (a constant), throughout the whole surface in question.

Now equilibrium is reached after the surface-contraction has done its utmost, that is to say when it has reduced the surface to the least possible area. So we arrive at the conclusion, from the physical side, that a surface such that $1/R + 1/R' = C$, in other words a surface which has the same *mean curvature* at all points, is equivalent to a surface of minimal area for the volume enclosed†;

* This simple but immensely important formula is due to Laplace (*Mécanique Céleste*, Bk x, suppl. *Théorie de l'action capillaire*, 1806).

† A surface may be “minimal” in respect of the area occupied, or of the volume enclosed: the former being such as the surface which a soap-film forms when it fills up a ring, whether plane or no. The geometers are apt to restrict the term “minimal surface” to such as these, or, more generally, to all cases where the mean curvature is *nil*; the others, being only minimal with respect to the volume contained, they call “surfaces of constant mean curvature.”

and to the same conclusion we may also come by ways purely mathematical. The plane and the sphere are two obvious examples of such surfaces, for in both the radius of curvature is everywhere constant.

From the fact that we may extend a soap-film across any ring of wire, however fantastically the wire be bent, we see that there is no end to the number of surfaces of minimal area which may be constructed or imagined*. While some of these are very complicated indeed, others, such as a spiral or helicoid screw, are relatively simple. But if we limit ourselves to *surfaces of revolution* (that is to say, to surfaces symmetrical about an axis), we find, as Plateau was the first to shew, that those which meet the case are few in number. They are six in all, namely the plane, the sphere, the cylinder, the catenoid, the unduloid, and a curious surface which Plateau called the nodoid.

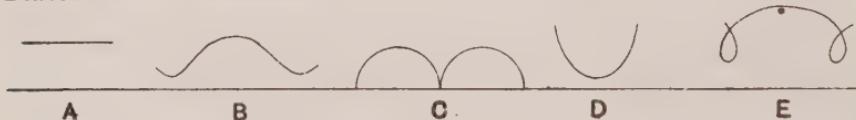


Fig. 104. Roulettes of the conic sections.

These several surfaces are all closely related, and the passage from one to another is generally easy. Their mathematical inter-relation is expressed by the fact (first shewn by Delaunay†, in 1841) that the plane curves by whose revolution they are generated are themselves generated as "roulettes" of the conic sections.

Let us imagine a straight line, or axis, on which a circle, ellipse or other conic section rolls; the focus of the conic section will describe a line in some relation to the fixed axis, and this line (or roulette), when we rotate it around the axis, will describe in space one or another of the six surfaces of revolution of which we are speaking.

If we imagine an ellipse so to roll on a base-line, either of its foci will describe a sinuous or wavy line (Fig. 104, *B*) at a distance

* To fit a minimal surface to the boundary of any given closed curve in space is a problem formulated by Lagrange, and commonly known as the "problem of Plateau," who solved it with his soap-films.

† Sur la surface de révolution dont la courbure moyenne est constante, *Journ. de M. Liouville*, vi, p. 309, 1841. Cf. (*int. al.*) J. Clerk Maxwell, On the theory of rolling curves, *Trans. R.S.E.* xvi, pp. 519–540, 1849; J. K. Wittemore, Minimal surfaces of rotation, *Ann. Math.* (2), xix, 1917, *Amer. Journ. Math.* xl, p. 69, 1918; Gino Loria, *Courbes planes spéciales, théorie et histoire*, Milan, 574 pp., 1930.

alternately maximal and minimal from the axis; this wavy line, by rotation about the axis, becomes the meridional line of the surface which we call the *unduloid*, and the more unequal the two axes are of our ellipse, the more pronounced will be the undulating sinuosity of the roulette. If the two axes be equal, then our ellipse becomes a circle; the path described by its rolling centre is a straight line parallel to the axis (*A*), and the solid of revolution generated therefrom will be a *cylinder*: in other words, the cylinder is a "limiting case" of the unduloid. If one axis of our ellipse vanish, while the other remains of finite length, then the ellipse is reduced to a straight line with its foci at the two ends, and its roulette will appear as a succession of semicircles touching one another upon the axis (*C*); the solid of revolution will be a series of equal *spheres*. If as before one axis of the ellipse vanish, but the other be infinitely long, then the roulette described by the focus of this ellipse will be a circular arc at an infinite distance; i.e. it will be a straight line normal to the axis, and the surface of revolution traced by this straight line turning about the axis will be a *plane*. If we imagine one focus of our ellipse to remain at a given distance from the axis, but the other to become infinitely remote, that is tantamount to saying that the ellipse becomes transformed into a parabola; and by the rolling of this curve along the axis there is described a catenary (*D*), whose solid of revolution is the *catenoid*.

Lastly, but this is more difficult to imagine, we have the case of the hyperbola. We cannot well imagine the hyperbola rolling upon a fixed straight line so that its focus shall describe a continuous curve. But let us suppose that the fixed line is, to begin with, asymptotic to one branch of the hyperbola, and that the rolling proceeds until the line is now asymptotic to the other branch, that is to say touching it at an infinite distance; there will then be mathematical continuity if we recommence rolling with this second branch, and so in turn with the other, when each has run its course. We shall see, on reflection, that the line traced by one and the same focus will be an "elastic curve," describing a succession of kinks or knots (*E*), and the solid of revolution described by this meridional line about the axis is the so-called *nodoid*.

The physical transition of one of these surfaces into another can

be experimentally illustrated by means of soap-bubbles, or better still, after another method of Plateau's, by means of a large globule of oil, supported when necessary by wire rings, and lying in a fluid of specific gravity equal to its own.

To prepare a mixture of alcohol and water of a density precisely equal to that of the oil-globule is a troublesome matter, and a method devised by Mr C. R. Darling is a great improvement on Plateau's*. Mr Darling used the oily liquid orthooulidene, which does not mix with water, has a beautiful and conspicuous red colour, and has precisely the same density as water when both are kept at a temperature of 24° C. We have therefore only to run the liquid into water at this temperature in order to produce beautifully spherical drops of any required size: and by adding a little salt to the lower layers of water, the drop may be made to rest or float upon the denser liquid.



Fig. 105.

We have seen that the soap-bubble, spherical to begin with, is transformed into a plane when we release its internal pressure and let the film shrink back upon the orifice of the pipe. If we blow a bubble and then catch it up on a second pipe, so that it stretches between, we may draw the two pipes apart, with the result that the spheroidal surface will be gradually flattened in a longitudinal direction, and the bubble will be transformed into a cylinder. But if we draw the pipes yet farther apart, the cylinder narrows in the middle into a sort of hour-glass form, the increasing curvature of its transverse section being balanced by a gradually increasing negative curvature in the longitudinal section; the cylinder has, in turn, been converted into an unduloid. When we hold a soft glass tube in the flame and "draw it out," we are in the same identical fashion converting a cylinder into an unduloid (Fig. 105, A); when on the other hand we stop the end and blow, we again convert the cylinder into an unduloid (B), but into one which is now positively, while the former was negatively, curved. The two figures are

* See *Liquid Drops and Globules*, 1914, p. 11. Robert Boyle used turpentine in much the same way; for other methods see Plateau, *op. cit.* p. 154.

essentially the same, save that the two halves of the one change places in the other.

That spheres, cylinders and unduloids are of the commonest occurrence among the forms of small unicellular organisms or of individual cells in the simpler aggregates, and that in the processes of growth, reproduction and development transitions are frequent from one of these forms to another, is obvious to the naturalist*, and we shall deal presently with a few of these phenomena. But before we go further in this enquiry we must consider, to some small extent at least, the *curvatures* of the six different surfaces, so far as to determine what modification is required, in each case, of the general equation which applies to them all. We shall find that with this question is closely connected the question of the *pressures* exercised by or impinging on the film, and also the very important question of the limiting conditions which, from the nature of the case, set bounds to the extension of certain of the figures. The whole subject is mathematical, and we shall only deal with it in the most elementary way.

We have seen that, in our general formula, the expression $1/R + 1/R' = C$, a constant; and that this is, in all cases, the condition of our surface being one of minimal area. That is to say, it is always true for one and all of the six surfaces which we have to consider; but the constant C may have any value, positive, negative or nil.

In the case of the plane, where R and R' are both infinite, $1/R + 1/R' = 0$. The expression therefore vanishes, and our dynamical equation of equilibrium becomes $P = p$. In short, we can only have a plane film, or we shall only find a plane surface in our cell, when on either side thereof we have equal pressures or no pressure at all; a simple case is the plane partition between two equal and similar cells, as in a filament of *Spirogyra*.

In the sphere the radii are all equal, $R = R'$; they are also positive, and $T(1/R + 1/R')$, or $2T/R$, is a positive quantity, involving a constant positive pressure P , on the other side of the equation.

In the cylinder one radius of curvature has the finite and positive value R ; but the other is infinite. Our formula becomes T/R , to

* They tend to reappear, no less obviously, in those precipitated structures which simulate organic form in the experiments of Leduc, Herrera and Lillie.

which corresponds a positive pressure P , supplied by the surface-tension as in the case of the sphere, but evidently of just half the magnitude.

In plane, sphere and cylinder the two principal curvatures are constant, separately and together; but in the unduloid the curvatures change from one point to another. At the middle of one of the swollen "beads" or bubbles, the curvatures are both positive; the expression $(1/R + 1/R')$ is therefore positive, and it is also finite. The film exercises (like the cylinder) a positive pressure inwards, to be compensated by an equivalent outward pressure from within. Between two adjacent beads, at the middle of one of the narrow necks, there is obviously a much stronger curvature in the transverse direction; but the total pressure is unchanged, and we now see that a negative curvature *along* the unduloid balances the increased curvature in the transverse direction. The sum of the two must remain positive as well as constant; therefore the convex or positive curvature must always be greater than the concave or negative curvature at the same point, and this is plainly the case in our figure of the unduloid.

The catenoid, in this respect a limiting case of the unduloid, has its curvature in one direction equal and opposite to its curvature in the other, this property holding good for all points of the surface; $R = -R'$; and the expression becomes

$$(1/R + 1/R') = (L/R - 1/R) = 0.$$

That is to say, the mean curvature is zero, and the catenoid, like the plane itself, has *no curvature*, and exerts no pressure. None of the other surfaces save these two share this remarkable property; and it follows that we may have at times the plane and the catenoid co-existing as parts of one and the same boundary system, just as the cylinder or the unduloid may be capped by portions of spheres. It follows also that if we stretch a soap-film between two rings, and so form an annular surface open at both ends, that surface is a catenoid: the simplest case being when the rings are parallel and normal to the axis of the figure*.

* A topsail bellied out by the wind is not a catenoid surface, but in vertical section it is everywhere a catenary curve; and Dürer shews beautiful catenary curves in the wrinkles under an Old Man's eyes. A simple experiment is to invert

The nodoid is, like the unduloid, a continuous curve which keeps altering its curvature as it alters its distance from the axis; but in this case the resultant pressure inwards is negative instead of positive. But this curve is a complicated one, and its full mathematical treatment is too hard for us.

In one of Plateau's experiments, a bubble of oil (protected from gravity by a fluid of equal density to its own) is balanced between annuli; and by adjusting the distance apart of these, it may be brought to assume the form of Fig. 106, that is to say, of a cylinder with spherical ends; there is then everywhere a pressure inwards on the fluid contents of the bubble a pressure due to the convexity

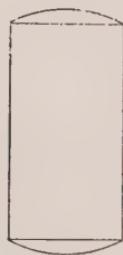


Fig. 106.

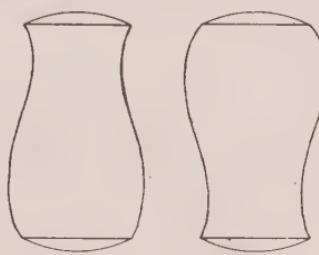


Fig. 107.

of the surface film. This cylinder may be converted into an unduloid, either by drawing the rings farther apart or by abstracting some of the oil, until at length rupture ensues, and the cylinder breaks up into two spherical drops. Or again, if the surrounding liquid be made ever so little heavier or lighter than that which constitutes the drop, then gravity comes into play, the conditions of equilibrium are modified accordingly, and the cylinder becomes part of an unduloid, with its dilated portion above or below as the case may be (Fig. 107).

In all cases the unduloid, like the original cylinder, is capped by spherical ends, the sign and the consequence of a positive pressure produced by the curved walls of the unduloid. But if our initial cylinder, instead of being tall, be a flat or dumpy one

a small funnel in a large one, wet them with soap-solution, and draw them apart; the film which develops between them is a catenoid surface, set perpendicularly to the two funnels. On this and other geometrical illustrations of the fact that a soap-film sets itself at right angles to a solid boundary, see an elegant paper by Mary E. Sinclair, in *Annals of Mathematics*, VIII, 1907.

(with certain definite relations of height to breadth), then new phenomena may occur. For now, if oil be cautiously withdrawn from the mass by help of a small syringe, the cylinder may be made to flatten down so that its upper and lower surfaces become plane: which is of itself a sufficient indication that the pressure inwards is now *nil*. But at the very moment when the upper and lower surfaces become plane, it will be found that the sides curve inwards, in the fashion shewn in Fig. 108 B. This figure is a catenoid, which,

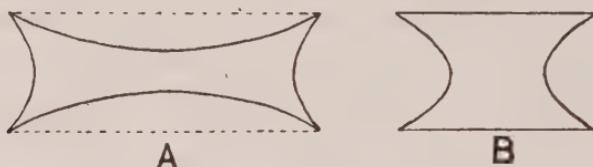


Fig. 108.

as we have seen, is, like the plane itself, a surface exercising no pressure, and which therefore may coexist with the plane as part of one and the same system.

We may continue to withdraw more oil from our bubble, drop by drop, and now the upper and lower surfaces dimple down into concave portions of spheres, as the result of the *negative* internal pressure; and thereupon the peripheral catenoid surface alters its form (perhaps, on this small scale, imperceptibly), and becomes a portion of a nodoid. It represents, in fact, that portion of the nodoid

which in Fig. 109 lies between such points as *O*, *P*. While it is easy to draw the outline, or meridional section, of the nodoid, it is obvious that the solid of revolution to be derived from it can never be realised in its entirety: for one part of the solid figure would cut, or entangle with, another. All that we can ever do, accordingly, is to realise isolated portions of the nodoid*.

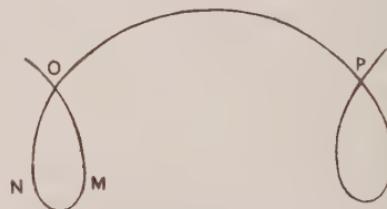


Fig. 109.

* This curve resembles the looped Elastic Curve (see Thomson and Tait, II, p. 148, fig. 7), but has its axis on the other side of the curve. The nodoid was represented upside-down in the first edition of this book, a mistake into which others have fallen, including no less a person than Clerk Maxwell, in his article "Capillarity" in the *Encycl. Brit.* 9th ed.

In all these cases the ring or annulus is not merely a means of mechanical restraint, controlling the form of the drop or bubble; it also marks the boundary, or "locus of discontinuity," between one surface and another.

If, in a sequel to the preceding experiment of Plateau's, we use solid discs instead of annuli, we may exert pressure on our oil-globule as we exerted traction before. We begin again by adjusting the pressure of these discs so that the oil assumes the form of a cylinder: our discs, that is to say, are adjusted to exercise a mechanical pressure just equal to what in the former case was supplied by the surface-tension of the spherical caps or ends of the bubble. If we now increase the pressure slightly, the peripheral walls become convexly curved, exercising a precisely corresponding pressure; the form assumed by the sides of our figure is now that of a portion of an unduloid. If we increase the pressure, the peripheral surface of oil will bulge out more and more, and will presently constitute a portion of a sphere. But we may continue the process yet further, and find within certain limits the system remaining perfectly stable. What is this new curved surface which has arisen out of the sphere, as the latter was produced from the unduloid? It is no other than a portion of a nodoid, that part which in Fig. 109 lies between *M* and *N*. But this surface, which is concave in both directions towards the surface of the oil within, is exerting a pressure upon the latter, just as did the sphere out of which a moment ago it was transformed; and we had just stated, in considering the previous experiment, that the pressure inwards exerted by the nodoid was a negative one. The explanation of this seeming discrepancy lies in the simple fact that, if we follow the outline of our nodoid curve in Fig. 109, from *OP*, the surface concerned in the former case, to *MN*, that concerned in the present, we shall see that in the two experiments the surface of the liquid is not the same, but lies on the positive side of the curve in the one case, and on the negative side in the other.

These capillary surfaces of Plateau's form a beautiful example of the "materialisation" of mathematical law. Theory leads to certain equations which determine the position of points in a system, and these points we may then plot as curves on a coordinate diagram; but a drop or a bubble may realise in an instant the

whole result of our calculations, and materialise our whole apparatus of curves. Such a case is what Bacon calls a "collective instance," bearing witness to the fact that one common law is obeyed by every point or particle of the system. Where the underlying equations are unknown to us, as happens in so many natural configurations, we may still rest assured that kindred mathematical laws are being automatically followed, and rigorously obeyed, and sometimes half-revealed.

Of all the surfaces which we have been describing, the sphere is the only one which can enclose space of itself; the others can only help to do so, in combination with one another or with the sphere. Moreover, the sphere is also, of all possible figures, that which encloses the greatest volume with the least area of surface*; it is strictly and absolutely the surface of minimal area, and it is, *ipso facto*, the form which will be assumed by a unicellular organism (just as by a raindrop), if it be practically homogeneous and if, like *Orbulina* floating in the ocean, its surroundings be likewise homogeneous and its field of force symmetrical†. It is only relatively speaking that the rest of these configurations are surfaces *minimae areae*; for they are so under conditions which involve various pressures or restraints. Such restraints are imposed by the pipe or annulus which supports and confines our oil-globule or soap-bubble; and in the case of the organic cell, similar restraints are supplied by solidifications partial or complete, or other modifications local or general, of the cell-surface or cell-wall.

One thing we must not fail to bear in mind. In the case of the soap-bubble we look for stability or instability, equilibrium or non-equilibrium, in its several configurations. But the living cell is seldom in equilibrium. It is continually using or expending energy; and this ceaseless flow of energy gives rise to a "steady state," taking the place of and simulating equilibrium. In like manner the

* On the circle and sphere as giving the smallest boundary for a given content, see (e.g.) Jacob Steiner, *Einfache Beweisen der isoperimetrischen Hauptsätze*, Berlin. *Abhandlungen*, 1836, pp. 123-132.

† The essential conditions of homogeneity and symmetry are none too common, and a spherical organism is only to be looked for among simple things. The floating (or pelagic) eggs of fishes, the spores of red seaweeds, the oospheres of *Fucus* or *Oedogonium*, the plasma-masses escaping from the cells of *Vaucheria*, are among the instances which come to mind.

hardly changing outline of a jet or waterfall is but in pseudo-equilibrium; it is in a steady state, dynamically speaking. Many puzzling and apparent paradoxes of physiology, such (to take a single instance) as the maintenance of a constant osmotic pressure on either side of a cell-membrane, are accounted for by the fact that energy is being spent and work done, and a *steady state* or pseudo-equilibrium maintained thereby.

Before we pass to biological illustrations of our surface-tension figures we have still another matter to deal with. We have seen from our description of two of Plateau's classical experiments, that at some particular point one type of surface gives place to another; and again we know that, when we draw out our soap-bubble into a cylinder, and then beyond, there comes a certain point at which the bubble breaks in two, and leaves us with two bubbles of which each is a sphere or a portion of a sphere. In short there are certain limits to the *dimensions* of our figures, within which limits equilibrium is stable, but at which it becomes unstable, and beyond which it breaks down. Moreover, in our composite surfaces, when the cylinder for instance is capped by two spherical cups or lenticular discs, there are well-defined ratios which regulate their respective curvatures and their respective dimensions. These two matters we may deal with together.

Let us imagine a liquid drop which in appropriate conditions has been made to assume the form of a cylinder; we have already seen that its ends will be capped by portions of spheres. Since one and the same liquid film covers the sides and ends of the drop (or since one and the same delicate membrane encloses the sides and ends of the cell), we assume the surface-tension (T) to be everywhere identical; and it follows, since the internal fluid-pressure is also everywhere identical, that the expression $(1/R + 1/R')$ for the cylinder is equal to the corresponding expression, which we may call $(1/r + 1/r')$, in the case of the terminal spheres. But in the

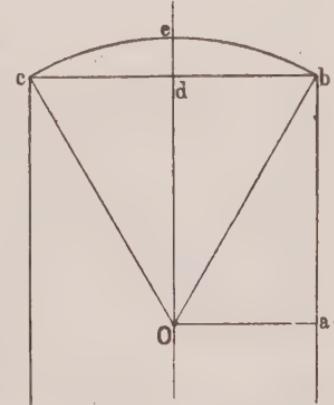


Fig. 110.

cylinder $1/R' = 0$, and in the sphere $1/r = 1/r'$. Therefore our relation of equality becomes $1/R = 2/r$, or $r = 2R$; which means that the sphere in question has just twice the radius of the cylinder of which it forms a cap.

And if Ob , the radius of the sphere, be equal to twice the radius (Oa) of the cylinder, it follows that the angle aOb is an angle of 60° , and bOc is also an angle of 60° ; that is to say, the arc bc is equal to $\frac{1}{3}\pi$. In other words, the spherical disc which (under the given conditions) caps our cylinder is not a portion taken at haphazard, but is neither more nor less than that portion of a sphere which is subtended by a cone of 60° . Moreover, it is plain that the height of the spherical cap, de , $= Ob - ab = R(2 - \sqrt{3}) = 0.27R$, where R is the radius of our cylinder, or one-half the radius of our spherical cap: in other words the normal height of the spherical cap over the end of the cylindrical cell is just a very little more than one-eighth of the diameter of the cylinder, or of the radius of the sphere. And these are the proportions which we recognise, more or less, under normal circumstances, in such a case as the cylindrical cell of *Spirogyra*, when one end is free and capped by a portion of a sphere*.

Among the many theoretical discoveries which we owe to Plateau, one to which we have just referred is of peculiar importance: namely that, with the exception of the sphere and the plane, the surfaces with which we have been dealing are only in complete equilibrium within certain dimensional limits, or in other words, have a certain definite limit of stability; only the plane and the sphere, or any portion of a sphere, are perfectly stable, because they are perfectly symmetrical, figures.

Perhaps it were better to say that their symmetry is such that any small disturbance will probably readjust itself, and leave the plane or spherical surface as it was before, while in the other configurations the chances are that a disturbance once set up will travel in one direction or another, increasing as it goes. For equilibrium and probability (as Boltzman told us) are nearly allied:

* The conditions of stability of the cylinder, and also of the catenoid, are explained with the utmost simplicity by Clerk Maxwell, in his article, already quoted, on "Capillarity." On the catenoids, see A. Terquem. *C.R.* xcii, pp. 407-9, 1881.

so nearly that that state of a system which is most likely to occur, or most likely to endure, is precisely that which we call the state of equilibrium.

For experimental demonstration, the case of the cylinder is the simplest. If we construct a liquid cylinder, either by drawing out a bubble or by supporting a globule of oil between two rings, the experiment proceeds easily until the length of the cylinder becomes just about three times as great as its diameter. But soon afterwards instability begins, and the cylinder alters its form; it narrows at

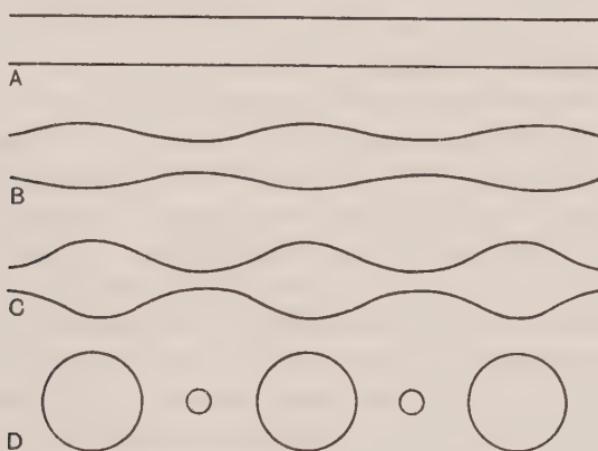


Fig. 111.

the waist, so passing into an unduloid, and the deformation progresses quickly until our cylinder breaks in two, and its two halves become portions of spheres. This physical change of one surface into another corresponds to what the mathematicians call a "discontinuous solution" of a problem of minima. The theoretical limit of stability, according to Plateau, is when the length of the cylinder is equal to its circumference, that is to say, when $L = 2\pi r$, or when the ratio of length to diameter is represented by π .

The fact is that any small disturbance takes the form of a wave, and travels along the cylinder. Short waves do not affect the stability of the system; but waves whose length exceeds that of the circumference tend to grow in amplitude: until, contracting here, expanding there, the cylinder turns into a pronounced unduloid, and soon breaks into two parts or more. Thus the cylinder is a

stable figure until it becomes longer than its own circumference, and then the risk of rupture may be said to begin. But Rayleigh shewed that still longer waves, leading to still greater instability, are needed to break down material resistance*. For, as Plateau knew well, his was a theoretical result, to be departed from under material conditions; it is affected largely by viscosity, and, as in the case of a flowing cylinder or jet, by inertia. When inertia plays a leading part, viscosity being small, the node of maximum instability corresponds to nearly half as much again as in the simple or theoretical case: and this result is very near to what Plateau himself had deduced from Savart's experiments on jets of water†. When the fluid is external (as when the cylinder is of air) the wave-length of maximal instability is longer still. Lastly, when viscosity is very large, and becomes paramount, then the wave-length between regions of maximal instability may become very long indeed: so that (as Rayleigh put it) "long (viscid) threads do not tend to divide themselves into drops at mutual distances comparable with the diameter of the cylinder, but rather to give way by attenuation at few and distant places." It is this that renders possible the making of long glass tubes, or the spinning of threads of "viscose" and like materials; but while these latter preserve their continuity, the principle of Plateau tends to give them something of a wavy, unduloid surface, to the great enhancement of their beauty. We are prepared, then, to find that such cylinders and unduloids as occur in organic nature seldom approach in regularity to those which theory prescribes or a soap-film may be made to shew; but rather exhibit all manner of gradations, from something exquisitely neat and regular to a coarse and distant approximation to the ideal thing‡.

The unduloid has certain peculiar properties as regards its limitations of stability, but we need mention two facts only: (1) that when the unduloid, which we produce with our soap-bubble or our

* Rayleigh, On the instability of fluid surfaces, *Sci. Papers*, III, p. 594.

† Cf. E. Tylor, *Phil. Mag.* xvi, pp. 504–518, 1933.

‡ Cf. F. Savart, Sur la constitution des veines liquides lancées par des orifices, etc., *Ann. de Chimie*, LIII, pp. 337–386, 1833. Rayleigh, On the instability of a cylinder of viscous liquid, etc., *Phil. Mag.* (5), xxxiv, 1892, or *Sci. Papers*, I, p. 361. See also Larmor, On the nature of viscid fluid threads, *Nature*, July 11, 1936, p. 74.

oil-globule, consists of the figure containing a complete constriction, then it has somewhat wide limits of stability; but (2) if it contain the swollen portion, then equilibrium is limited to the case of the figure consisting of one complete unduloid, no less nor more; that is to say when the ends of the figure are constituted by the narrowest portions, and its middle by the widest portion of the entire curve. The theoretical proof of this is difficult; but if we take the proof for granted, the fact itself will serve to throw light on what we have learned regarding the stability of the cylinder. For, when we remember that the meridional section of our unduloid is generated by the rolling of an ellipse upon a straight line in its own plane, we easily see that the length of the entire unduloid is equal to the circumference of the generating ellipse. As the unduloid becomes less and less sinuous in outline it approaches, and in time reaches, the form of the cylinder, as a "limiting case"; and *pari passu*, the ellipse which generated it passes into a circle, as its foci come closer and closer together. The cylinder of a length equal to the circumference of its generating circle is homologous to an unduloid whose length is equal to the circumference of its generating ellipse; and this is just what we recognise as constituting one complete segment of the unduloid.

The cylinder turns so easily into an unduloid, and the unduloid is capable of assuming so many graded differences of form, that we may expect to find it abundantly and variously represented among the simpler living things. For the same reason it is the very stand-by of the glass-blower, whose flasks and bottles are, of necessity, unduloids*. The blown-glass bottle is a true unduloid, and the potter's vase a close approach to an unduloid; but the alabaster bottle, turned on the lathe, is another story. It may be an imitation, or a reminiscence, of the potter's or the glass-blower's work; but it is no unduloid nor any surface of minimal area at all.

The catenoid, as we have seen, is a surface of zero pressure, and as such is unlikely to form part (unless momentarily) of the closed boundary of a cell. It forms a limiting case between unduloid and nodoid, and, were it realised; it would seldom be visibly different from the other two. In *Trichodina pediculus*, a minute infusorian para-

* Unless, that is to say, their shape be cramped and their mathematical beauty annihilated, by compression in a mould.

site of the freshwater polype, we have a circular disc bounded (apparently) by two parallel rings of cilia, with a pulley-like groove



Fig. 112. *Trichodina pediculus*.

“gullet,” gives no assurance of a zero pressure; and we must take it that the equatorial groove of *Trichodina* resembles, or approaches, but is not mathematically identical with, a catenoid surface.

While those figures of equilibrium which are also surfaces of revolution are only six in number, there is an infinite number of other figures of equilibrium, that is to say of surfaces of constant mean curvature, which are not surfaces of revolution; and it can be shewn mathematically that any given contour can be occupied by a finite portion of some one such surface, in stable equilibrium. The experimental verification of this theorem lies in the simple fact (already noted) that however we bend a wire into a closed curve, plane or not plane, we may always fill the entire area with a continuous film. No more interesting problem has ever been propounded to mathematicians as the outcome of experiment than the general problem so to describe a minimal surface passing through a closed contour; and no complete solution, no general method of approach, has yet been discovered*.

Of the regular figures of equilibrium, or surfaces of constant mean curvature, apart from the surfaces of revolution which we have discussed, the helicoid spiral is the most interesting to the biologist.

* Partial solutions, closely connected with recent developments of mathematical analysis, are due to Riemann, Weierstrass and Schartz. Cf. (*int. al.*) G. Darboux, *Théorie des surfaces*, 1914, pp. 490–601; T. Bonneson, *Problèmes des isopérimètres et des isépiplanes*, Paris, 1929; Hilbert's *Anschauliche Geometrie*, 1932, p. 237 seq.; a good account also in G. A. Bliss's *Calculus of Variations*, Chicago, 1925. See also (*int. al.*) Tibor Radó, *Mathem. Ztschr.* xxxii, 1930; Jesse Douglas, *Amer. Math. Journ.* xxxiii, 1931, *Journ. Math. Phys.* xv, 1936.

This is a helicoid generated by a straight line perpendicular to an axis, about which it turns at a uniform rate, while at the same time it slides, also uniformly, along this same axis. At any point in this surface, the curvatures are equal and of opposite sign, and the sum of the curvatures is accordingly nil. Among what are called "ruled surfaces," or surfaces capable of being defined by a system of stretched strings*, the plane and the helicoid are the only two whose mean curvature is null, while the cylinder is the only one whose curvature is finite and constant. As this simplest of helicoids corresponds, in three dimensions, to what in two dimensions is merely a plane (the latter being generated by the rotation of a straight line about an axis without the superadded gliding motion which generates the helicoid), so there are other and much more complicated helicoids which correspond to the sphere, the unduloid and the rest of our figures of revolution, the generating planes of these latter being supposed to wind spirally about an axis. In the case of the cylinder it is obvious that the resulting figure is indistinguishable from the cylinder itself. In the case of the unduloid we obtain a grooved spiral, and we meet with something very like it in nature (for instance in Spirochaetes, *Bodo gracilis*, etc.); but in point of fact, the screw motion given to an unduloid or catenary curve fails to give a minimal screw surface, as we might have expected it to do.

The foregoing considerations deal with a small part only of the theory of surface-tension, or capillarity: with that part, namely, which relates to the surfaces capable of subsisting in equilibrium under the action of that force, either of itself or subject to certain simple constraints. And as yet we have limited ourselves to the case of a single surface, or of a single drop or bubble, leaving to another occasion a discussion of the forms assumed when such drops or vesicles meet and combine together. In short, what we have said may help us to understand the form of a *cell*—considered, as with certain limitations we may legitimately consider it, as a liquid drop or liquid vesicle; the conformation of a *tissue* or cell-aggregate must be dealt with in the light of another series of theoretical considerations. In both cases, we can do no more than touch on the fringe of a large and difficult subject. There are many forms

* Or rather, surfaces such that through every point there runs a straight line which lies wholly in the surface.

capable of realisation under surface-tension, and many of them doubtless to be recognised among organisms, which we cannot deal with in this elementary account. The subject is a very general one; it is, in its essence, more mathematical than physical; it is part of the mathematics of surfaces, and only comes into relation with surface-tension because this physical phenomenon illustrates and exemplifies, in a concrete way, the simple and symmetrical conditions with which the mathematical theory is capable of dealing. And before we pass to illustrate the physical phenomena by biological examples, we must repeat that the simple physical conditions which we presuppose will never be wholly realised in the organic cell. Its substance will never be a perfect fluid, and hence equilibrium will be slowly reached; its surface will seldom be perfectly homogeneous, and therefore equilibrium will seldom be perfectly attained; it will very often, or generally, be the seat of other forces, symmetrical or unsymmetrical; and all these causes will more or less perturb the surface-tension effects*. But we shall find that, on the whole, these effects of surface-tension though modified are not obliterated nor even masked; and accordingly the phenomena to which I have devoted the foregoing pages will be found manifestly recurring and repeating themselves among the phenomena of the organic cell.

In a spider's web we find exemplified several of the principles of surface-tension which we have now explained. The thread is spun out of a glandular secretion which issues from the spider's body as a semi-fluid cylinder, the force of expulsion giving it its length and that of surface-tension giving it its circular section. It is too viscid, and too soon hardened on exposure to the air, to break up into drops or spherules; but it is otherwise with another sticky secretion which, coming from another gland, is simultaneously poured over the

* That "every particular that worketh any effect is a thing compounded more or less of diverse single natures, more manifest and more obscure" is a point made and dwelt on by Bacon. Of the same principle a great astronomer speaks as follows: "It is one of the fundamental characteristics of natural science that we *never get beyond an approximation*... Nature *never offers us simple and undivided phenomena to observe, but always infinitely complex compounds of many different phenomena.* Each single phenomenon can be described mathematically in terms of the accepted fundamental laws of Nature:... but we can never be sure that we have carried the analysis to its full exhaustion, and have isolated one single simple phenomenon." W. de Sitter, in *Nature*, Jan. 21, 1928, p. 99.

slacker cross-threads as they issue to form the spiral portion of the web. This latter secretion is more fluid than the first, and only dries up after several hours*. By capillarity it "wets" the thread, spreading over it in an even film or liquid cylinder. As such it has its limits of stability, and tends to disrupt at points more distant than the theoretical wave-length, owing to the imperfect fluidity of the viscous film and still more to the frictional drag of the inner thread with which it is in contact. Save for this qualification the cylinder disrupts in the usual manner, passing first into the wavy outline of an unduloid, whose swollen internodes swell more and more till the necks between them break asunder, and leave a row of spherical drops or beads strung like dewdrops at regular intervals along the thread. If we try to varnish a thin taut wire we produce automatically the same identical result†; unless our varnish be such as to dry almost instantaneously it gathers into beads, and do what we will we fail to spread it smooth. It follows that, according to the drying qualities of our varnish, the process may stop at any point short of the formation of perfect spherules; and as our final stage we may only obtain half-formed beads or the wavy outlines of an unduloid. The beads may be helped to form by jerking the stretched thread, and so disturbing the unstable equilibrium of the viscid cylinder. This the spider has been said to do, but Dr G. T. Bennett assures me that she does nothing of the kind. She only draws her thread out a little, and leaves it a trifle slack; if the gum should break into droplets, well and good, but it matters little. The web with its sticky threads is not improved thereby. Another curious phenomenon here presents itself.

In Plateau's experimental separation of a cylinder of oil into two spherical halves, it was noticed that, when contact was nearly broken, that is to say when the narrow neck of the unduloid had become very thin, the two spherical bullae, instead of absorbing the fluid out of the narrow neck into themselves as they had done with the preceding portion, drew out this small remaining part of

* When we see a web bespangled with dew of a morning, the dewdrops are not drops of pure water, but of water mixed with the sticky, gummy fluid of the cross-threads; the radii seldom if ever shew dewdrops. See F. Strehlke, Beobachtungen an Spinnengewebe, *Poggendorff's Annalen*, XL, p. 146, 1937.

† Felix Plateau recommends the use of a weighted thread or plumb-line, to be drawn up slowly out of a jar of water or oil; *Phil. Mag.* xxxiv, p. 246, 1867.

the liquid into a thin thread as they completed their spherical form and receded from one another: the reason being that, after the thread or "neck" has reached a certain tenuity, internal friction prevents or retards a rapid exit of the fluid from the thread to the adjacent spherule. It is for the same reason that we are able to draw a glass rod or tube, which we have heated in the middle, into a long and uniform cylinder or thread by quickly separating the two ends. But in the case of the glass rod the long thin thread quickly cools and solidifies, while in the ordinary separation of a liquid cylinder the corresponding intermediate cylinder remains liquid; and therefore, like any other liquid cylinder, it is liable to



Fig. 113. Dew-drops on a spider's web.

break up, provided that its dimensions exceed the limit of stability. And its length is generally such that it breaks at two points, thus leaving two terminal portions continuous and confluent with the spheres, and one median portion which resolves itself into a tiny spherical drop, midway between the original and larger two. Occasionally, the same process of formation of a connecting thread repeats itself a second time, between the small intermediate spherule and the large spheres; and in this case we obtain two additional spherules, still smaller in size, and lying one on either side of our first little one. This whole phenomenon, of equal and regularly interspaced beads, often with little beads regularly interspaced between the larger ones, and now and then with a third order of still smaller beads regularly intercalated, may be easily observed in a spider's web, such as that of *Epeira*, very often with beautiful regularity—sometimes interrupted and disturbed by a slight want of homogeneity in the secreted fluid; and the same phenomenon is

repeated on a grosser scale when the web is bespangled with dew, and its threads bestrung with pearls innumerable. To the older naturalists, these regularly arranged and beautifully formed globules on the spider's web were a frequent source of wonderment. Blackwall, counting some twenty globules in a tenth of an inch, calculated that a large garden-spider's web should comprise about 120,000 globules; the net was spun and finished in about forty minutes, and Blackwall was filled with admiration of the skill and quickness with which the spider manufactured these little beads. And no wonder, for according to the above estimate they had to be made at the rate of about 50 per second*.

Here we see exemplified what Plateau told us of the law of minimal areas transforming the cylinder into the unduloid and disrupting it

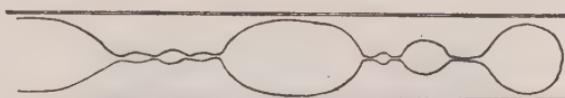


Fig. 114. Root-hair of *Trianea*, in glycerine. After Berthold.

into spheres. The little delicate beads which stud the long thin pseudopodia of a foraminifer, such as *Gromia*, or which appear in like manner on the film of protoplasm coating the long radiating spicules of *Globigerina*, represent an identical phenomenon. Indeed we may study in a protoplasmic filament the whole process of formation of such beads: if we squeeze out on a slide the viscid contents of a mistletoe-berry, the long sticky threads into which the substance runs shew the whole phenomenon particularly well. True, many long cylindrical cells, such as are common in plants, shew no sign of beading or disruption; but here the cell-walls are never fluid but harden as they grow, and the protoplasm within is kept in place and shape by its contact with the cell-wall. It was noticed many years ago by Hofmeister†, and afterwards explained by Berthold, that if we dip the long root-hairs of certain water-plants, such as *Hydrocharis* or *Trianea*, in a denser fluid (a little sugar-solution or

* J. Blackwall, *Spiders of Great Britain* (Ray Society), 1859, p. 10; *Trans. Linn. Soc.* xvi, p. 477, 1833. On the strength and elasticity of the spider's web, see J. R. Benton, *Amer. Journ. Science*, xxiv, pp. 75–78, 1907.

† *Lehrbuch von der Pflanzenzelle*, p. 71; cf. Nägeli, *Pflanzenphysiologische Untersuchungen (Spirogyra)*, III, p. 10.

dilute glycerine), the cell-sap tends to diffuse outwards, the protoplasm parts company with its surrounding and supporting wall, and then lies free as a protoplasmic cylinder in the interior of the cell. Thereupon it soon shews signs of instability, and commences to disrupt; it tends to gather into spheres, which however, as in our illustration, may be prevented by their narrow quarters from assuming the complete spherical form; and in between these spheres, we have more or less regularly alternate ones, of smaller size*. We could not wish for a better or a simpler proof of the *essential fluidity* of the protoplasm†. Similar, but less regular, beads or droplets may be caused to appear, under stimulation by an alternating current, in the protoplasmic threads within the living cells of the hairs of *Tradescantia*; the explanation usually given is, that the viscosity of the protoplasm is reduced, or its fluidity increased; but an increase of the surface-tension would seem a more likely reason‡.

In one of Robert Chambers's delicate experiments, a filament of protoplasm is drawn off, by a micro-needle, from the fluid surface of a starfish-egg. If drawn too far it breaks, and part returns within the protoplasm while the other rounds itself off on the needle's point. If drawn out less far, it looks like a row of beads or chain of droplets; if yet more relaxed, the droplets begin to fuse until the whole filament is withdrawn; if drawn out anew the process repeats itself. The whole story is a perfect description of the behaviour of a fluid jet or cylinder, of varying length and thickness§.

We may take note here of a remarkable series of phenomena, which, though they seem at first sight to be of a very different order,

* The intermediate spherules appear with great regularity and beauty whenever a liquid jet breaks up into drops. So a bursting soap-bubble scatters a shower of droplets all around, sometimes all alike, but often with a beautiful alternation of great and small. How the breaking up of thread or jet into drops may be helped, regularised, and sometimes complicated, by external vibrations is another and by no means unimportant story.

† Though doubtless to speak of the viscid thread as a fluid is but a first approximation; cf. Larmor, in *Nature*, July 11, 1936.

‡ Kühne, *Untersuchungen über das Protoplasma*, 1864, p. 75, etc.

§ Cf. R. Chambers in *Colloid Chemistry, theoretical and applied*, II, cap. 24, 1928; also *Ann. de Physiol.* VI, p. 234, 1930; etc.

are closely related to those which attend and which bring about the breaking-up of a liquid cylinder or thread.

In Mr Worthington's beautiful experiments on splashes*, it was found that the fall of a round pebble into water from a height first formed a dip or hollow in the surface, and then caused a filmy "cup" of water to rise up all round, opening out trumpet-fashion

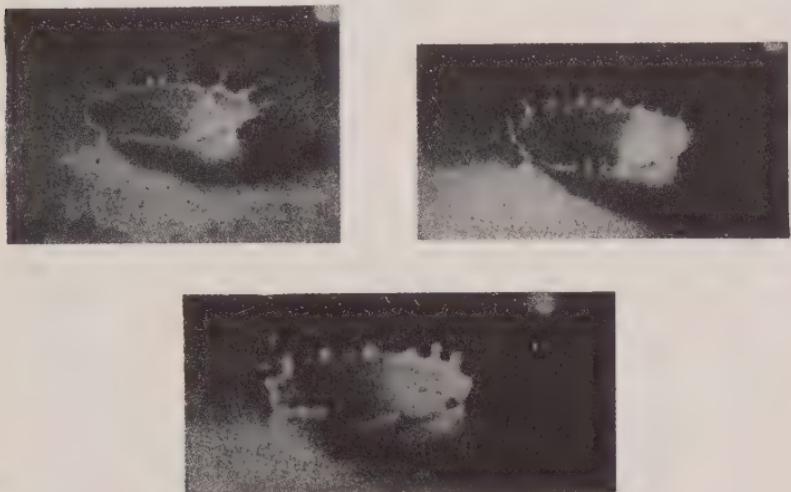


Fig. 115. Phases of a splash. From Worthington.

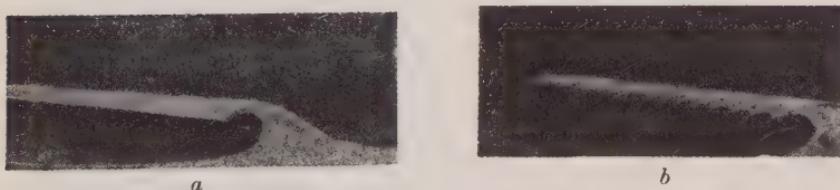


Fig. 116. A wave breaking into spray.

or closing in like a bubble, according to the height from which the pebble fell. The cup or "crater" tends to be fluted in alternate ridges and grooves, its edges get scolloped into corresponding lobes and notches, and the projecting lobes or prominences tend to break off or break up into drops or beads (Fig. 115). A similar appearance is seen on a great scale in the edge of a breaking wave: for the smooth

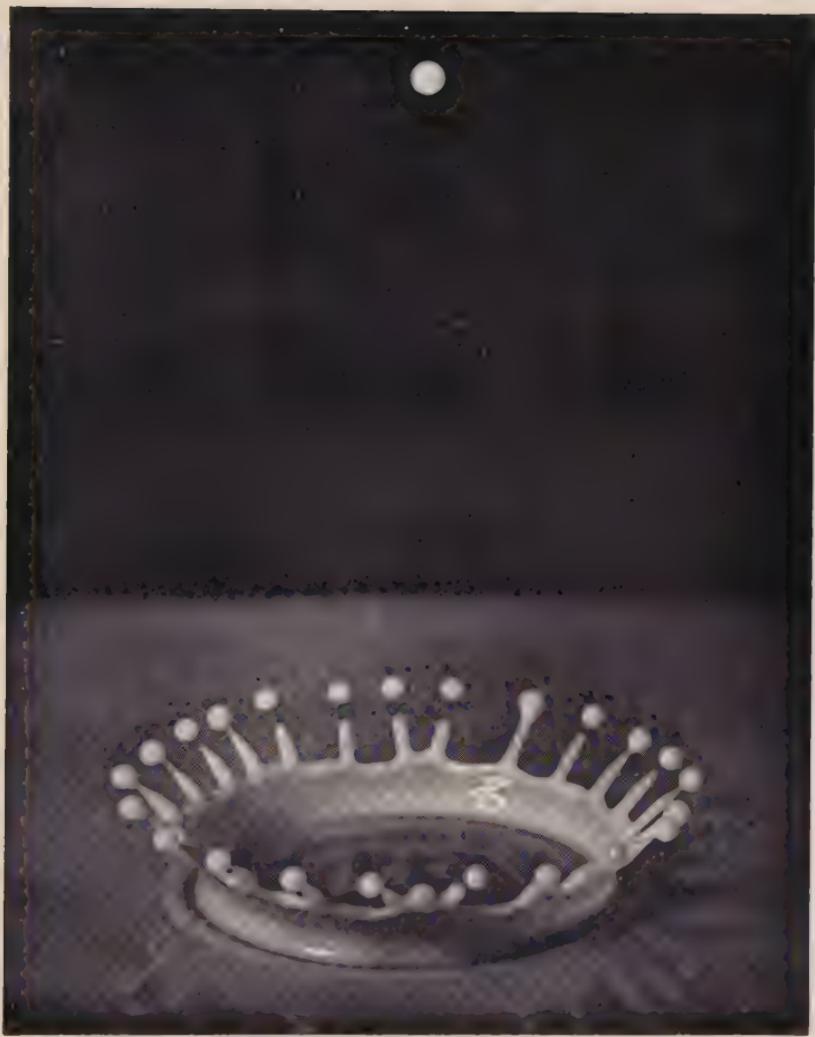
* *A Study of Splashes*, 1908, p. 38, etc.; also various papers in *Proc. R.S.* 1876-1882, and *Phil. Trans. (A)*, 1897 and 1900.

edge becomes notched or sinuous, and the surface near by becomes ribbed or fluted, owing to the internal flow being helped here and hindered there by a viscous shear; and then all of a sudden the uneven edge shoots out an array of tiny jets, which break up into the countless droplets which constitute "spray" (Fig. 116). The naturalist may be reminded also of the beautifully symmetrical notching of the calycles of many hydroid zoophytes, which little cups had begun their existence as liquid or semi-liquid films before they became stiff and rigid. The next phase of the splash (with which we are less directly concerned) is that the crater subsides, and where it stood a tall column rises up, which also tends, if it be tall enough, to break up into drops. Lastly the column sinks down in its turn, and a ripple runs out from where it stood.

The edge of our little cup forms a liquid ring or annulus, comparable on the one hand to the edge of an advancing wave, and on the other to a liquid thread or cylinder if only we conceive the thread to be bent round into a ring; and accordingly, just as the thread segments first into an unduloid and then into separate spherical drops, so likewise will the edge of cup or annulus tend to do. This phase of notching, or beading, of the edge of the splash is beautifully seen in many of Worthington's experiments*, and still more beautifully in recent work (Frontispiece†). In the second place the fact that the crater rises up means that liquid is flowing in from below; the segmentation of the rim means that channels of easier flow are being created, along which the liquid is led or driven into the protuberances; and these last are thereby exaggerated into the jets or streams which become conspicuous at the edge of the crater. In short any film or film-like fluid or semi-fluid cup will be unstable; its instability will tend to show itself in a fluting of the surface and a notching of the edge; and just such a fluting and notching are conspicuous features of many minute organic cup-like structures. In the hydroids (Fig. 117), we see that these common features of the

* Cf. *A Study of Splashes*, pp. 17, 77. The same phenomenon is often well seen in the splash of an oar. It is beautifully and continuously evident when a strong jet of water from a tap impinges on a curved surface and then shoots off again.

† We owe this picture to the kindness of Mr Harold E. Edgerton, of the Massachusetts Institute of Technology. It shews the splash caused by a drop falling into a thin layer of milk; a second drop of milk is seen above, following the first. The exposure-time was 1/50,000 of a second.



An instantaneous photograph of a 'splash' of milk. From Harold E. Edgerton,
Massachusetts Technical Institution

cup and the annulation of the stem are phenomena of the same order. A cord-like thickening of the edge of the cup is a variant of the same order of phenomena; it is due to the checking at the rim of the flow of liquid from below, and a similar thickening is to be seen, not only in some hydroid calyces but also in many Vorticellae (cf. Fig. 124) and other cup-shaped organisms. And these are by no means the only manifestations of surface-tension in a splash which shew resemblances and analogies to organic form*.

The phenomena of an ordinary liquid splash are so swiftly transitory that their study is only rendered possible by photography:

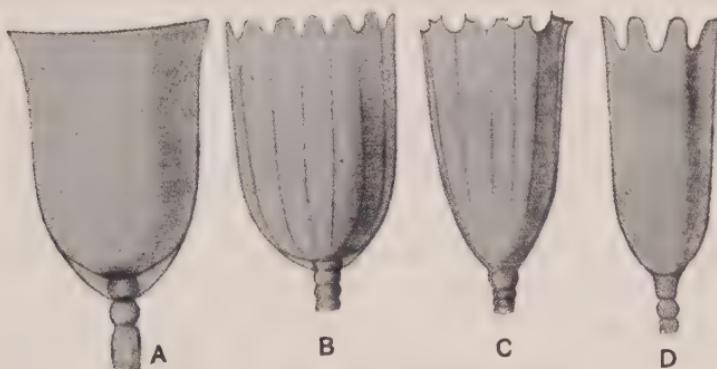


Fig. 117. Calyces of *Campanularia* spp.

but this excessive rapidity is not an essential part of the phenomenon. For instance, we can repeat and demonstrate many of the simpler phenomena, in a permanent or quasi-permanent form, by splashing water on to a surface of dry sand†, or by firing a bullet into a soft metal target. There is nothing, then, to prevent a slow and lasting manifestation, in a viscous medium such as a protoplasmic organism, of phenomena which appear and disappear with

* The same phenomena are modified in various ways, and the drops are given off much more freely, when the splash takes place in an electric field—all owing to the general instability of an electrified liquid surface; and a study of this aspect of the subject might suggest yet more analogies with organic form. Cf. J. Zeleny, *Phys. Rev.* x, 1917; J. P. Gott, *Proc. Cambridge Philos. Soc.* xxxi, 1935; etc.

† We find now and then in certain brick-clays of glacial origin, hard, quoit-shaped rings, each with an equally indurated, round or flattened ball resting on it. These may be precisely imitated by splashing large drops of water on a smooth surface of fine dry sand. The ring corresponds, apparently, to the crater of the splash, and the ball (or its water content) to the pillar rising in the middle.

evanescent rapidity in a more mobile liquid. Nor is there anything peculiar in the splash itself; it is simply a convenient method of setting up certain motions or currents, and producing certain surface-forms, in a liquid medium—or even in such an imperfect fluid as a bed of sand. Accordingly, we have a large range of possible conditions under which the organism might conceivably display configurations analogous to, or identical with, those which Mr Worthington has shewn us how to exhibit by one particular experimental method.

To one who has watched the potter at his wheel, it is plain that the potter's thumb, like the glass-blower's blast of air, depends for its efficacy upon the physical properties of the clay or "slip" it works on, which for the time being is essentially a fluid. The cup and the saucer, like the tube and the bulb, display (in their simple and primitive forms) beautiful surfaces of equilibrium as manifested under certain limiting conditions. They are neither more nor less than glorified "splashes," formed slowly, under conditions of restraint which enhance or reveal their mathematical symmetry. We have seen, and we shall see again before we are done, that the art of the glass-blower is full of lessons for the naturalist as also for the physicist: illustrating as it does the development of a host of mathematical configurations and organic conformations which depend essentially on the establishment of a constant and uniform pressure within a *closed* elastic shell or fluid envelope or bubble. In like manner the potter's art illustrates the somewhat obscurer and more complex problems (scarcely less frequent in biology) of a figure of equilibrium which is an *open* surface of revolution. The two series of problems are closely akin; for the glass-blower can make most things which the potter makes, by cutting off *portions* of his hollow ware; besides, when this fails and the glass-blower, ceasing to blow, begins to use his rod to trim the sides or turn the edges of wineglass or of beaker, he is merely borrowing a trick from the still older craft of the potter.

It would seem venturesome to extend our comparison with these liquid surface-tension phenomena from the cup or calycle of the hydrozoon to the little hydroid polyp within: and yet there is something to be learned by such a comparison. The cylindrical body of the tiny polyp, the jet-like row of tentacles, the beaded

annulations which these tentacles exhibit, the web-like film which sometimes (when they stand a little way apart) conjoins their bases, the thin annular film of tissue which surrounds the little organism's mouth, and the manner in which this annular "peristome" contracts*, like a shrinking soap-bubble, to close the aperture, are every one of them features to which we may find a singular and striking parallel in the surface-tension phenomena of the splash†.

Some seventy years ago much interest was aroused by Helmholtz's work (and also Kirchhoff's) on "discontinuous motions of a fluid‡"; that is to say, on the movements of one body of fluid within another, and the resulting phenomena due to friction at the surfaces between. What Kelvin§ called Helmholtz's "admirable discovery of the law of vortex-motion in a perfect fluid" was the chief result of this investigation; and was followed by much experimental work, in order to illustrate and to extend the mathematical conclusions.

The drop, the bubble and the splash are parts of a long story; and a "falling drop," or a drop moving through surrounding fluid, is a case deserving to be considered. A drop of water, tinged with fuchsin, is gently released (under a pressure of a couple of millimetres) at the bottom of a glass of water||. Its momentum enables it to rise through a few centimetres of the surrounding water, and in doing so it communicates motion to the water around. In front the rising drop *thrusts* its way through, almost like a solid body; behind it tends to *drag* the surrounding water after it, by fluid friction¶; and these two motions together give rise to beautiful vorticoïd configurations, the *Strömungspilze* or *Tintenpilze* of their first discoverers (Fig. 119). Under a higher and more continuous pressure

* See a *Study of Splashes*, p. 54.

† There is little or no difference between a *splash* and a *burst bubble*. The craters of the moon have been compared with, and explained by, both of these.

‡ Helmholtz, in *Berlin. Monatsber.* 1868, pp. 215–228; Kirchhoff, in *Crelle's Journal*, LXX, pp. 289–298, LXXI, 237–273, 1869–70.

§ W. Thomson, in *Proc. R.S.E.* VI, p. 94, 1867.

|| See A. Overbeck, "Ueber discontinuirliche Flüssigkeitsbewegungen, *Wiedemann's Annalen*, II, 1877; W. Bezold, "Ueber Strömungsfiguren in Flüssigkeiten, *ibid.* XXIV, pp. 569–593, 1885; P. Czermak, *ibid.* I, p. 329, 1893; etc.

¶ The frictional drag on the hinder part of the drop is felt alike in the ship, the bird and the aeroplane, and tends to produce retarding vortices in them all. It is always minimised in one way or another, and it is automatically minimised in the present instance, as the drop thins off and tapers down.

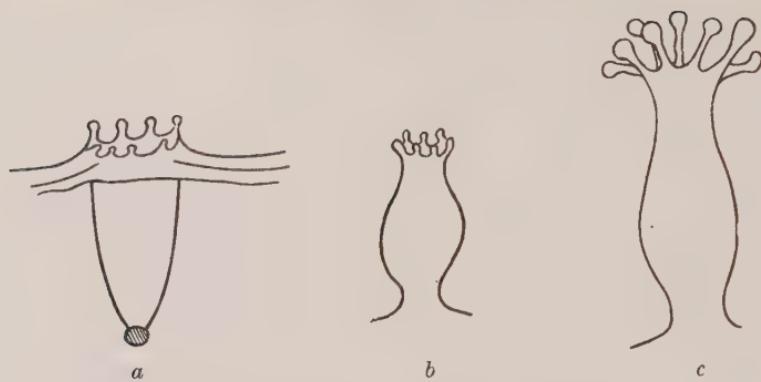


Fig. 118. *a, b.* More phases of a splash, after Worthington.
c. A hydroid polype, after Allman.

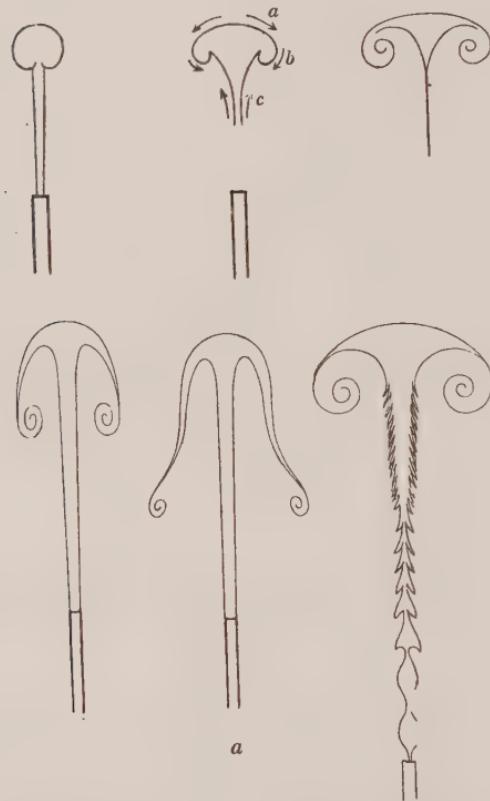


Fig. 119. Liquid jets. From A. Overbeck.

the drop becomes a jet; the form of the vortex is modified thereby, and may be further modified by slight differences of temperature (i.e. of density), or by interrupting the rate of flow. To let a drop of ink fall into water is a simple and most beautiful experiment*. The effect is more violent than in the former case. The descending

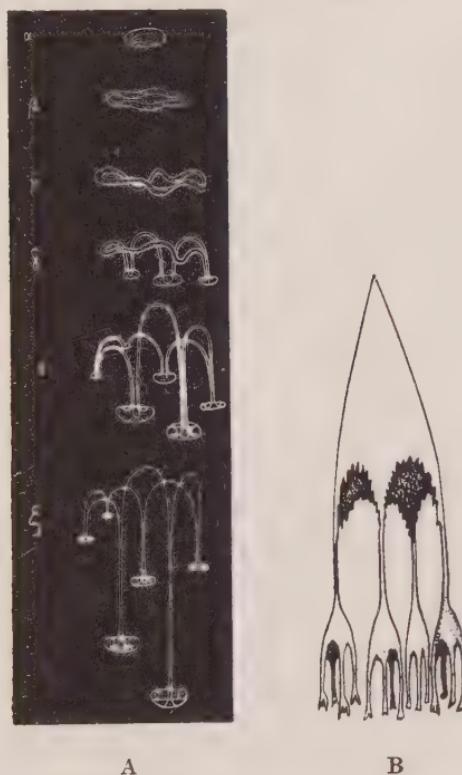


Fig. 120. Falling drops. A, ink in water, after J. J. Thomson and Newall.
B, fusel oil in paraffin, after Tomlinson.

drop turns into a complete vortex-ring; it expands and attenuates; it waves about, and the descending loops again turn into incipient vortices (Fig. 120).

Lastly, instead of letting our drop rise or fall freely, we may use a hanging drop, which, while it sinks, remains suspended to the surface. Thus it cannot form a complete annulus, but only a

* J. J. Thomson and H. F. Newall, On the formation of vortex-rings by drops, *Proc. R.S.* xxxix, pp. 417–436, 1885. Emil Hatschek, On forms assumed by a gelatinising liquid in various coagulating solutions, *ibid.* (A) xciv, pp. 303–316, 1918.

partial vortex suspended by a thread or column—just as in Overbeck's jet-experiments; and the figure so produced, in either case, is closely analogous to that of a medusa or jellyfish, with its bell or "umbrella," and its clapper or "manubrium" as well. Some years ago Emil Hatschek made such vortex-drops as these of liquid gelatine dropped into a hardening fluid. These "artificial medusae" sometimes show a symmetrical pattern of radial "ribs", due to shrinkage, and this to dehydration by the coagulating fluid. An

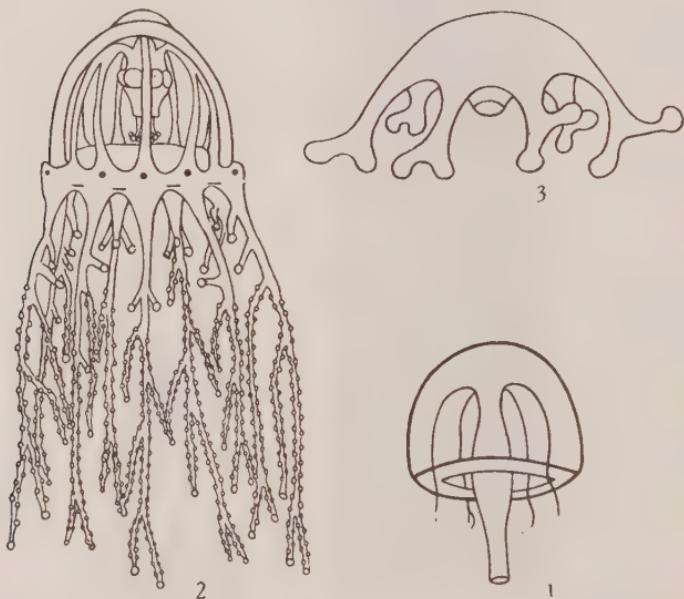


Fig. 121. Various medusoids: 1, *Syncoryne*; 2, *Cordylophora*; 3, *Cladonema* (after Allman).

extremely curious result of Hatschek's experiments is to shew how sensitive these vorticoid drops are to physical conditions. For using the same gelatine all the while, and merely varying the density of the fluid in the third decimal place, we obtain a whole range of configurations, from the ordinary hanging drop to the same with a ribbed pattern, and then to medusoid vortices of various graded forms.

The living medusa has a geometrical symmetry so marked and regular as to suggest a physical or mechanical element in the little creature's growth and construction. It has, to begin with, its vortex-like bell or umbrella, with its cylindrical handle or manubrium. The bell is

traversed by radial canals, four or in multiples of four; its edge is beset with tentacles, smooth or often beaded, at regular intervals and of graded sizes; and certain sensory structures, including solid concretions or "otoliths," are also symmetrically interspaced. No sooner made, than it begins to pulsate; the little bell begins to "ring."

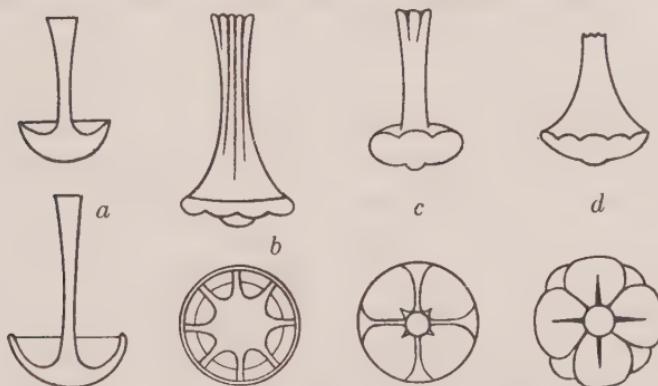


Fig. 121b. "Medusoid drops", of gelatin. After Hatschek.

Buds, miniature replicas of the parent-organism, are very apt to appear on the tentacles, or on the manubrium or sometimes on the edge of the bell; we seem to see one vortex producing others before our eyes. The development of a medusoid deserves to be studied without prejudice, from this point of view. Certain it is that the tiny medusoids of *Obelia*, for instance, are budded off with a rapidity and a complete perfection which suggest an automatic and all but instantaneous act of conformation, rather than a gradual process of growth.

Moreover, not only do we recognise in a vorticoid drop a "schema" or analogue of medusoid form, but we seem able to discover various actual phases of the splash or drop in the all but innumerable living types of jellyfish; in *Cladonema* we seem to see an early stage of a breaking drop, and in *Cordylophora* a beautiful picture of incipient vortices. It is hard indeed to say how much or little all these analogies imply. But they indicate, at the very least, how certain simple organic forms might be naturally assumed by one fluid mass within another, when gravity, surface tension and fluid friction play



Fig. 122. *Medusachloris*, a ciliate infusoria.

their part, under balanced conditions of temperature, density and chemical composition.

A little green infusorian from the Baltic Sea is, as near as may be, a medusa in miniature*. It is curious indeed to find the same medusoid, or as we may now call it vorticoid, configuration occurring in a form so much lower in the scale, and so much less in order of magnitude, than the ordinary medusae.

According to Plateau, the viscosity of the liquid, while it retards the breaking up of the cylinder and increases the length of the segments beyond that which theory demands, has nevertheless less influence in this direction than we might have expected. On the other hand any external support or adhesion, or mere contact with a solid body, will be equivalent to a reduction of surface-tension and so will very greatly increase the stability of our cylinder. It is for this reason that the mercury in our thermometers seldom separates into drops: though it sometimes does so, much to our inconvenience. And again it is for this reason that the protoplasm in a long tubular or cylindrical cell need not divide into separate cells and internodes until the length of these far exceeds the theoretical limits.

An interesting case is that of a viscous drop immersed in another viscous fluid, and drawn out into a thread by a shearing motion of the latter. The thread seems stable at first, but when left to rest it breaks up into drops of a very definite and uniform size, the size of the drops, or wave-length of the unduloid of which they are made, depending on the relative viscosities of the two threads†.

Plateau's results, though discovered by way of experiment and though (as we have said) they illustrate the "materialisation" of mathematical law, are nevertheless essentially theoretical results approached rather than realised in material systems. That a liquid cylinder begins to be unstable when its length exceeds $2\pi r$ is all but mathematically true of an all but immaterial soap-bubble; but very far from true, as Plateau himself was well aware, in a flowing jet, retarded by viscosity and by inertia. The principle is true and universal; but our living cylinders do not follow the abstract laws

* *Medusachloris phiale*, of A. Pascher, *Biol. Centralbl.* xxxvii, pp. 421–429, 1917.

† See especially Rayleigh, *Phil. Mag.* xxxiv, p. 145, 1892, by whom the subject is carried much further than where Plateau left it. See also (*int. al.*) G. I. Taylor, *Proc. R.S. (A)*, cxlvi, p. 501, 1934; S. Tomotika, *ibid. cl.*, p. 322, 1935; etc.

of mathematics, any more than do the drops and jets of ordinary fluids or the quickly drawn and quickly cooling tubes in the glass-worker's hands.

Plateau says that in most liquids the influence of viscosity is such as to cause the cylinder to segment when its length is about four times, or even six times, its diameter, instead of a fraction over three times, as theory would demand of a perfect fluid. If we take it at four times, the resulting spherules would have a diameter of about 1·8 times, and their distance apart would be about 2·2 times, the original diameter of the cylinder; and the calculation is not difficult which would shew how these dimensions are altered in the case of a cylinder formed around a solid core, as in the case of a spider's web. Plateau also observed that the *time* taken in the division of the cylinder is directly proportional to its diameter, while varying with the nature of the liquid. This question, of the time taken in the division of a cell or filament in relation to its dimensions, has not so far as I know been enquired into by biologists.

From the simple fact that the sphere is of all configurations that whose surface-area for a given volume is an absolute minimum, we have seen it to be the one figure of equilibrium assumed by a drop or vesicle when no disturbing factor is at hand; but such freedom from counter-influences is likely to be rare, and neither does the rain-drop nor the round world itself retain its primal sphericity. For one thing, gravity will always be at hand to drag and distort our drop or bubble, unless its dimensions be so minute that gravity becomes insignificant compared with capillarity. Even the soap-bubble will be flattened or elongated by gravity, according as we support it from below or from above; and the bubble which is thinned out almost to blackness will, from its small mass, be the one which remains most nearly spherical*.

Innumerable new conditions will be introduced, in the shape of complicated tensions and pressures, when one drop or bubble becomes associated with another, and when a system of intermediate films or partition-walls is developed between them. This subject we shall discuss later, in connection with cell-aggregates or tissues, and we shall find that further theoretical considerations are

* Cf. Dewar, On soap-bubbles of long duration, *Proc. Roy. Inst.* Jan. 19, 1929.

needed as a preliminary to any such enquiry. Meanwhile let us consider a few cases of the forms of cells, either solitary, or in such simple aggregates that their individual form is little disturbed thereby. Let us clearly understand that the cases we are about to consider are those where the perfect symmetry of the sphere is replaced by another symmetry, less complete, such as that of an ellipsoidal or cylindrical cell. The cases of asymmetrical deformation or displacement, such as are illustrated in the production of a bud or the development of a lateral branch, are much simpler; for here we need only assume a slight and localised variation of surface-tension, such as may be brought about in various ways through the heterogeneous chemistry of the cell. But such diffused and graded asymmetry as brings about for instance the ellipsoidal shape of a yeast-cell is another matter.

If the sphere be the one surface of complete symmetry and therefore of independent equilibrium, it follows that in every cell which is otherwise conformed there must be some definite cause of its departure from sphericity; and if this cause be the obvious one of resistance offered by a solidified envelope, such as an egg-shell or firm cell-wall, we must still seek for the deforming force which was in action to bring about the given shape prior to the assumption of rigidity. Such a cause may be either external to, or may lie within, the cell itself. On the one hand it may be due to external pressure or some form of mechanical restraint, as when we submit our bubble to the partial restraint of discs or rings or more complicated cages of wire; on the other hand it may be due to intrinsic causes, which must come under the head either of differences of internal pressure, or of lack of homogeneity or isotropy in the surface or its envelope*.

* A case which we have not specially considered, but which may be found to deserve consideration in biology, is that of a cell or drop suspended in a liquid of *varying density*, for instance in the upper layers of a fluid (e.g. sea-water) at whose surface condensation is going on, so as to produce a steady density-gradient. In this case the normally spherical drop will be flattened into an oval form, with its maximum surface-curvature lying at the level where the densities of the drop and the surrounding liquid are just equal. The sectional outline of the drop has been shewn to be not a true oval or ellipse, but a somewhat complicated quartic curve. (*Rice, Phil. Mag.* Jan. 1915.) A more general case, which also may well deserve consideration by the biologist, is that of a charged bubble in (for instance) a uniform field of force: which will expand or elongate in the direction of the lines of force, and become a spheroidal surface in continuous transformation with the original sphere.

Our formula of equilibrium, or equation to an elastic surface, is $P = p_e + (T/R + T'/R')$, where P is the internal pressure, p_e any extraneous pressure normal to the surface, R , R' the radii of curvature at a point, and T , T' the corresponding tensions, normal to one another, of the envelope.

Now in any given form which we seek to account for, R , R' are known quantities; but all the other factors of the equation are subject to enquiry. And somehow or other, by this formula, we must account for the form of any solitary cell whatsoever (provided always that it be not formed by successive stages of solidification), the cylindrical cell of *Spirogyra*, the ellipsoidal yeast-cell, or (as we shall see in another chapter) even the egg of any bird. In using this formula hitherto we have taken it in a simplified form, that is to say we have made several limiting assumptions. We have assumed that P was the uniform hydrostatic pressure, equal in all directions, of a body of liquid; we have assumed likewise that the tension T was due to surface-tension in a homogeneous liquid film, and was therefore equal in all directions, so that $T = T'$; and we have only dealt with surfaces, or parts of a surface, where extraneous pressure, p_n , was non-existent. Now in the case of a bird's egg the external pressure p_n , that is to say the pressure exercised by the walls of the oviduct, will be found to be a very important factor; but in the case of the yeast-cell or the *Spirogyra*, wholly immersed in water, no such external pressure comes into play. We are accordingly left in such cases as these last with two hypotheses, namely that the departure from a spherical form is due to inequalities in the internal pressure P , or else to inequalities in the tension T , that is to say to a difference between T and T' . In other words, it is theoretically possible that the oval form of a yeast-cell is due to a greater internal pressure, a greater "tendency to grow" in the direction of the longer axis of the ellipse, or alternatively, that with equal and symmetrical tendencies to growth there is associated a difference of external resistance in respect of the tension, and implicitly the molecular structure, of the cell-wall. Now the former hypothesis is not impossible. Protoplasm is far from being a perfect fluid; it is the seat of various internal forces, sometimes manifestly polar, and it is quite possible that the forces, osmotic and other, which lead to an increase of the content of the

cell and are manifested in pressure outwardly directed upon its wall may be unsymmetrical, and such as to deform what would otherwise be a simple sphere. But while this hypothesis is not impossible, it is not very easy of acceptance. The protoplasm, though not a perfect fluid, has yet on the whole the properties of a fluid; within the small compass of the cell there is little room for the development of unsymmetrical pressures; and in such a case as *Spirogyra*, where most part of the cavity is filled by watery sap, the conditions are still more obviously, or more nearly, those under which a uniform hydrostatic pressure should be displayed. But in variations of T , that is to say of the specific surface-tension per unit area, we have an ample field for all the various deformations with which we shall have to deal. Our condition now is, that $(T/R + T'/R') = \text{a constant}$; but it no longer follows, though it may still often be the case, that this will represent a surface of absolute minimal area. As soon as T and T' become unequal, we are no longer dealing with a perfectly liquid surface film; but its departure from perfect fluidity may be of all degrees, from that of a slight non-isotropic viscosity to the state of a firm elastic membrane*; and it matters little whether this viscosity or semi-rigidity be manifested in the self-same layer which is still a part of the protoplasm of the cell, or in a layer which is completely differentiated into a distinct and separate membrane. As soon as, by secretion or adsorption, the molecular constitution of the surface-layer is altered, it is clearly conceivable that the alteration, or the secondary chemical changes which follow it, may be such as to produce an anisotropy, and to render the molecular forces less capable in one direction than another of exerting that contractile force by which they are striving to reduce to a minimum the surface area of the cell. A slight inequality in two opposite directions will produce the ellipsoid cell, and a great inequality will give rise to the cylindrical cell.

I take it therefore, that the cylindrical cell of *Spirogyra*, or any other cylindrical cell which grows in freedom from any manifest external restraint, has assumed that particular form simply by reason of the molecular constitution of its developing wall or

* Indeed any non-isotropic *stiffness*, even though T remained uniform, would simulate, and be indistinguishable from, a condition of non-stiffness and non-isotropic T .

membrane; and that this molecular constitution was anisotropic, in such a way as to render extension easier in one direction than another. Such a lack of homogeneity or of isotropy in the cell-wall is often rendered visible, especially in plant-cells, in the form of concentric lamellae, annular and spiral striations, and the like. But there exists yet another heterogeneity, to help us account for the long threads, hairs, fibres, cylinders, which are so often formed. Carl Nägeli said many years ago that organised bodies, starch-grains, cellulose and protoplasm itself, consisted of invisible particles, each an aggregate of many molecules—he called them *micellæ*; and these were isolated, or “dispersed” as we should say, in a watery medium. This theory was, to begin with, an attempt to account for the colloid state; but at the same time, the particles were supposed to be so ordered and arranged as to render the substance anisotropic, to confer on it vectorial properties as we say nowadays, and so to account for the polarisation of light by a starch-grain or a hair. It was so criticised by Bütschli and von Ebner that it fell into disrepute, if not oblivion; but a great part of it was true. And the micellar structure of wool, cotton, silk and similar substances is now rendered clearly visible by the same X-ray methods as revealed the molecular orientation, or lattice-structure, of a crystal to von Laue.

It is now well known that the cell-wall has in many cases a definite structure which depends on molecular assemblages in the material of which it is composed, and is made visible by X-rays in the form of “diffraction patterns”. The green alga *Valonia* has very large bubbly cells, 2–3 centimetres long, with cell-walls formed, as usual, of cellulose; this substance is a polysaccharide, with long-chain molecules some 500 Ångström-units, or say $0\cdot05\mu$ long, bound together sideways to form a multiple sheet or three-dimensional lattice. In the cell-wall of *Valonia* one set of chains runs round in a left-handed spiral, another forms meridians from pole to pole, and these two layers are superposed alternately to build the wall. Hemp has two layers, both running in right-handed spirals; flax two layers, crossing and recrossing in spirals of opposite sign. Even the cytoplasm and its contents seem to be influenced by molecular “*lignes directrices*,” corresponding to the striae of the cell-wall. Analogous but still more complicated results of molecular structure are to be found in wool, cotton and other fibres*.

* Cf. R. D. Preston, *Phil. Trans. (B)*, ccxiv, p. 131, 1934; Preston and Astbury, *Proc. R.S. (B)*, cxxii, pp. 76–97, 1937; and many other important papers by Astbury, van Iterson, Heyn, and others. We are brought by them to a borderland

But this phenomenon, while it brings about a certain departure from complete symmetry, is still compatible with, and coexistent with, many of the phenomena which we have seen to be associated with surface-tension. The symmetry of tensions still leaves the cell a solid of revolution, and its surface is still a surface of equilibrium. The fluid pressure within the cylinder still causes the film or membrane which caps its ends to be of a spherical form. And in the young cell, where the surface pellicle is absent or but little differentiated, as for instance in the oögonium of *Achlya* or in the young zygosporangium of *Spirogyra*, we see the tendency of the entire structure towards a spherical form reasserting itself: unless, as in the latter case, it be overcome by direct compression within the cylindrical mother-cell. Moreover, in those cases where the adult filament consists of cylindrical cells we see that the young germinating spore, at first spherical, very soon assumes with growth an elliptical or ovoid form—the direct result of an incipient anisotropy of its envelope, which when more developed will convert the ovoid into a cylinder. We may also notice that a truly cylindrical cell is comparatively rare, for in many cases what we call a cylindrical cell shews a distinct bulging of its sides; it is not truly a cylinder, but a portion of a spheroid or ellipsoid.

Unicellular organisms in general—protozoa, unicellular cryptogams, various bacteria and the free isolated cells, spores, ova, etc. of higher organisms—are referable for the most part to a small number of typical forms; but there are many others in which either no symmetry is to be recognised, or in which the form is clearly not one of equilibrium. Among these latter we have *Amoeba* itself and all manner of amoeboid organisms, and also many curiously shaped cells such as the Trypanosomes and various aberrant Infusoria. We shall return to the consideration of these; but in the meanwhile it will suffice to say (and to repeat) that, inasmuch as their surfaces are not equilibrium-surfaces, so neither are the living cells themselves in any stable equilibrium. On the contrary, they are in continual flux and movement, each portion of the

between chemical and histological structure, where micellae and long-chain molecules enlarge and alter our conceptions not only of cellulose and keratin, but of pseudopodia and cilia, of bone and muscle, and of the naked surface of the cell. See L. E. R. Picken, *The fine structure of biological systems*, *Biol. Reviews*, xv, pp. 133–67, 1940.

surface constantly changing its form, passing from one phase to another of an equilibrium which is never stable for more than a moment, and which death restores to the stable equilibrium of a sphere. The former class, which rest in stable equilibrium, must fall (as we have seen) into two classes—those whose equilibrium arises from liquid surface-tension alone, and those in whose conformation some other pressure or restraint has been superimposed upon ordinary surface-tension.

To the fact that all these organisms belong to an order of magnitude in which form is mainly, if not wholly, conditioned and controlled by molecular forces is due the limited range of forms which they actually exhibit. They vary according to varying physical conditions. Sometimes they do so in so regular and orderly a way that we intuitively explain them as “phases of a life-history,” and leave physical properties and physical causation alone: but many of their variations of form we treat as exceptional, abnormal, decadent or morbid, and are apt to pass these over in neglect, while we give our attention to what we call a typical or “characteristic” form or attitude. In the case of the smallest organisms, bacteria, micrococci, and so forth, the range of form is especially limited, owing to their minuteness, the powerful pressure which their highly curved surfaces exert, and the comparatively homogeneous nature of their substance. But within their narrow range of possible diversity these minute organisms are protean in their changes of form. A certain species will not only change its shape from stage to stage of its little “cycle” of life; but it will be remarkably different in outward form according to the circumstances under which we find it, or the histological treatment to which we subject it. Hence the pathological student, commencing the study of bacteriology, is early warned to pay little heed to differences of *form*, for purposes of recognition or specific identification. Whatever grounds we may have for attributing to these organisms a permanent or stable specific identity (after the fashion of the higher plants and animals), we can seldom safely do so on the ground of definite and always recognisable *form*: we may often be inclined, in short, to ascribe to them a physiological (sometimes a “pathogenic”) rather than a morphological specificity.

Many unicellular forms, and a few other simple organisms, are spherical, and serve to illustrate in the simplest way the point at issue. Unicellular algae, such as *Protococcus* or *Halisphaera*, the innumerable floating eggs of fishes, the floating unilocular foraminifer *Orbulina*, the lovely green multicellular *Volvox* of our ponds, all these in their several grades of simplicity or complication are so many round drops, spherical because no alien forces have deformed or mis-shapen them. But observe that, with the exception of *Volvox*, whose spherical body is covered wholly and uniformly with minute cilia, all the above are passive or inactive forms; and in a "resting" or encysted phase the spherical form is common and general in a great range of unicellular organisms.

Conversely, we see that those unicellular forms which depart markedly from sphericity—excluding for the moment the amoeboid

forms and those provided with skeletons—are all ciliate or flagellate. Cilia and flagella are *sui generis*; we know nothing of them from the physical side, we cannot reproduce or imitate them in any non-living drop or fluid surface. But we can easily see that they have an influence on *form*, besides serving for locomotion. When our little *Monad* or *Euglena* develops a flagellum, that is in itself an indication of asymmetry or "polarity," of non-homogeneity of the little cell; and

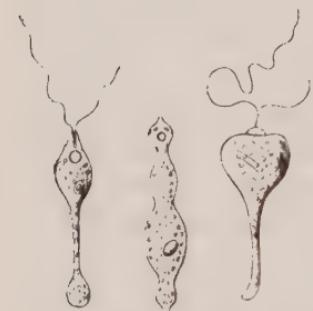


Fig. 123. A flagellate "monad,"
Distigma proteus Ehr.
After Saville Kent.

in the various flagellate types the flagellum or its analogues always stand on prominent points, or ends, or edges of the cell—on parts, that is to say, where curvature is high and surface-tension may be expected to be low—for the product of surface-tension by mean curvature tends to be constant.

The minute dimensions of a cilium or a flagellum are such that the molecular forces leading to surface-tension must here be under peculiar conditions and restraints; we cannot hope to understand them by comparison with a whip-lash, or through any other analogy drawn from a different order of magnitude. I suspect that a ciliary surface is always electrically charged, and that a point-charge is formed or induced in each cilium or flagellum. Just as we learn the properties of a drop or a jet as phenomena proper to their scale of magnitude, so some day we shall learn the very different physical, but

microcosmic, properties of these minute, mobile, pointed, fluid or semi-fluid threads.*

Cilia, like flagella, tend to occupy positions, or cover surfaces, which would otherwise be unstable; and often indeed (as in a trochosphere larva or even in a Rotifer) a ring of cilia seems to play the very part of one of Plateau's wire rings, supporting and steadyng the semi-fluid mass in its otherwise unstable configuration. Let us note here (in passing) what seems to be an analogous phenomenon. Chitinous hairs, spines or bristles are common and characteristic structures among the smaller Crustacea, and more or less generally among the Arthropods. We find them at every exposed point or corner; they fringe the sharp edge or border of a limb; as we draw the creature, we seem to know where to put them in! In short, they tend to occur, as the flagella do, just where the surface-tension would be lowest, if or when the surface was in a fluid condition.

Of the other surfaces of Plateau, we find cylinders enough and to spare in *Spirogyra* and a host of other filamentous algae and fungi. But it is to the vegetable kingdom that we go to find them, where a cellulose envelope enables the cylinder to develop beyond its ordinary limitations.

The unduloid makes its appearance whenever sphere or cylinder begin to give way. We see the transitory figure of an unduloid in the normal fission of a simple cell, or of the nucleus itself; and we have already seen it to perfection in the incipient beadings of a spider's web, or of a pseudopodial thread of protoplasm. A large number of infusoria have unduloid contours, in part at least; and this figure appears and reappears in a great variety of forms. The cups of various Vorticellae (Fig. 124), below the ciliated ring, look like a beautiful series of unduloids, in every gradation of form, from what is all but cylindrical to all but a perfect sphere; moreover successive phases in their life-history appear as mere graded changes

* It is highly characteristic of a cilium or a flagellum that neither is ever seen motionless, unless the cell to which it belongs is moribund. "I believe the motion to be ceaseless, unconscious and uncontrolled, a direct function of the chemical and physical environment"; George Bidder, in *Presidential Address to Section D, British Association*, 1927. Cf. also James Gray, *Proc. R.S. (B)*, xcix, p. 398, 1926.

of unduloid form. It has been shewn lately, in one or two instances at least, that species of *Vorticella* may "metamorphose" into one another: in other words, that contours supposed to characterise species are not "specific". These Vorticellid unduloids are

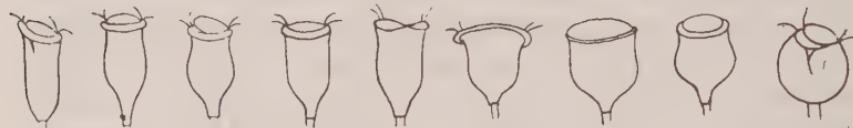


Fig. 124. Various species of *Vorticella*.

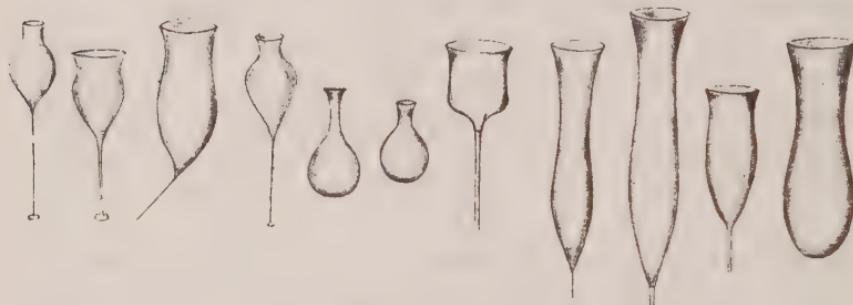


Fig. 125. Various species of *Salpingoeca*.

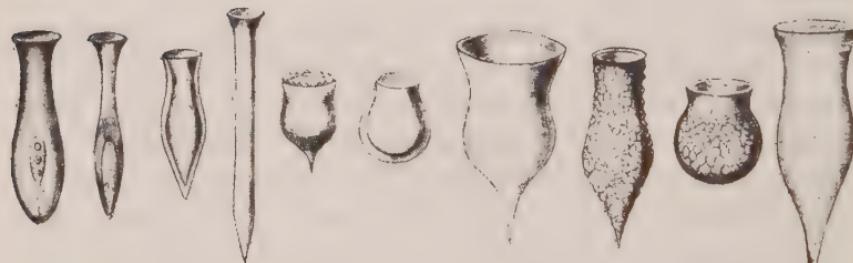


Fig. 126. Various species of *Tintinnus*, *Dinobryon* and *Codonella*.
After Saville Kent and others.

not fully symmetrical; rather are they such unduloids as develop when we suspend an oil-globule between two unequal rings; or blow a bubble between two unequal pipes. For our Vorticellid bell hangs by two terminal supports, the narrow stalk to which it is attached below, and the thickened ring from which spring its circumoral cilia; and it is most interesting to see how, when the bell leaves

its stalk (as sometimes happens) and swims away, a new ring of cilia comes into being, to encircle and support its narrow end.

Similar unduloids may be traced in even greater variety among other families or genera of the Infusoria. Sometimes, as in *Vorticella* itself, the unduloid is seen in the contour of the soft semifluid body of the living animal. At other times, as in *Salpingoeca*, *Tintinnus*, and many other genera, we have a membranous cup containing the animal, but originally secreted by, and moulded upon, its semifluid living surface. Here we have an excellent illustration of the contrast between the different ways in which such a structure may be regarded and interpreted. The teleological explanation is that it is developed for the sake of protection,



Fig. 127. *Vaginicola*.



Fig. 128. *Folliculina*.

as a domicile and shelter for the little organism within. The mechanical explanation of the physicist (seeking after the "efficient," not the "final" cause) is that it owes its presence, and its actual conformation, to certain chemico-physical conditions: that it was inevitable, under the given conditions, that certain constituent substances present in the protoplasm should be drawn by molecular forces to its surface layer; that under this adsorptive process, the conditions continuing favourable, the particles accumulated and concentrated till they formed (with the help of the surrounding medium) a pellicle or membrane, thicker or thinner as the case might be; that this surface pellicle or membrane was inevitably bound, by molecular forces, to contract into a surface of the least possible area which the circumstances permitted; that in the present case the symmetry and "freedom" of the system permitted, and *ipso facto* caused, this surface to be a surface of revolution; and that of the few surfaces of revolution which, as

being also surfaces *minimae areae*, were available, the unduloid was manifestly the one permitted, and *ipso facto* caused, by the dimensions of the organism and other circumstances of the case. And

just as the thickness or thinness of the pellicle was obviously a subordinate matter, a mere matter of degree, so we see that the actual outline of this or that particular unduloid is also a very subordinate matter, such as physico-chemical variants of a minor order would suffice to bring about; for between the various unduloids which the various species of *Vorticella* represent, there is no more real difference than that difference of ratio or degree which exists between two circles of different diameter, or two lines of unequal length.

In many cases (of which Fig. 129 is an example) we have a more or less unduloid form exhibited not by a surrounding pellicle or shell, but by the soft protoplasmic body of a ciliated organism; in such cases the form is mobile, and changes continually from one to another unduloid contour according to the movements of the animal.* We are dealing here with no stable equilibrium, but possibly with a subtle problem of "stream-lines," as in the difficult but beautiful problems suggested by the form of a fish. But this whole class of cases, and

Fig. 129. *Trachelophyllum*. After Wreszniowski.

of problems, we merely take note of here; we shall speak of them again, but their treatment is hard.

In considering such series of forms as these various unduloids we are brought sharply up (as in the case of our bacteria or micrococci) against the biological concept of organic *species*. In the intense classificatory activity of the last hundred years it has come about that every form which is apparently characteristic, that is to say which is capable of being described or portrayed, and of being

* Doflein lays stress, in like manner, on the fact that *Spirochaete*, unlike *Spirillum*, "ist nicht von einer starren Membran umhüllt," and that waves of contraction may be seen passing down its body.



recognised when met with again, has been recorded as a *species*—for we need not concern ourselves with the occasional discussions, or individual opinions, as to whether such and such a form deserves “specific rank,” or be “only a variety.” And this secular labour is pursued in direct obedience to the precept of the *Systema Naturae*—“*ut sic in summa confusione rerum apparenti, summus conspicatur Naturae ordo.*” In like manner the physicist records, and is entitled to record, his many hundred “species” of snow-crystals*, or of crystals of calcium carbonate. Indeed the snow-crystal illustrates to perfection how Nature rings the changes on every possible variation and permutation and combination of form: subject only to the condition (in this instance) that a snow-crystal shall be a plane, symmetrical, rectilinear figure, with all its external angles those of a regular hexagon. We may draw what we please on a sheet of “hexagonal paper,” keeping to its lines; and when we repeat our drawing, kaleidoscope-fashion, about a centre, the stellate figure so obtained is sure to resemble one or another of the many recorded species of snow-crystals. And this endless beauty of crystalline form is further enhanced when the flakes begin to thaw, and all their feathery outlines soften. But regarding these “species” of his, the physicist makes no assumptions: he records them *simpliciter*; he notes, as best he can, the circumstances (such as temperature or humidity) under which each occurs, in the hope of elucidating the conditions which determine their formation†; but above all, he

* The case of the snow-crystals is a particularly interesting one; for their “distribution” is analogous to what we find, for instance, among our microscopic skeletons of Radiolarians. That is to say, we may one day meet with myriads of some one particular form or species, and another day with myriads of another; while at another time and place we may find species intermingled in all but inexhaustible variety. Cf. e.g. J. Glaisher, *Illustrated London News*, Feb. 17, 1855; *Q.J.M.S.* III, pp. 179–185, 1855; Sir Edward Belcher, *Last of the Arctic Voyages*, II, pp. 288–306 (4 plates), 1855; William Scoresby, *An Account of the Arctic Regions*, Edinburgh, 1820; G. Hellmann, *Schneekristalle*, Berlin, 1893; Bentley and Humphreys, *Snow Crystals*, New York, 1931; and the especially beautiful figures of Nakaya and Hasikura in *Journ. Fac. Sci. Hokkaido*, Dec. 1934.

† Every snow-crystal tells, more or less plainly, the story of its own development. The cold upper air is saturated with water-vapour, but this is scanty and rarefied compared with the space in which snow-crystallisation is going on. Hence crystallisation tends to proceed only along the main axes, or cardinal framework, of the crystalline structure of ice; in so doing it gives a visible picture or actual embodiment of the trigonal-hexagonal space-lattice, in the endless permutations and combinations of its constituent elements.

does not introduce the element of time, and of succession, or discuss their origin and affiliation as an *historical* sequence of events. But in biology, the term species carries with it many large though often vague assumptions; though the doctrine or concept of the "permanence of species" is dead and gone, yet a certain quasi-permanency is still connoted by the term. If a tiny foraminiferal shell, a *Lagena* for instance, be found living to-day, and a shell indistinguishable from it to the eye be found fossil in the Chalk or some still more remote geological formation, the assumption is deemed legitimate that that species has "survived," and has handed down its minute specific character or characters from generation to generation, unchanged for untold millions of years*. If the ancient forms be like to rather than identical with the recent, we still assume an unbroken descent, accompanied by the hereditary transmission of common characters and progressive variations. And if two identical forms be discovered at the ends of the earth, still (with occasional slight reservations on the score of possible "homoplasy") we build hypotheses on this fact of identity, taking it for granted that the two appertain to a common stock, whose dispersal in space must somehow be accounted for, its route traced, its epoch determined, and its causes discussed or discovered. In short, the naturalist admits no exception to the rule that a *natural* classification can only be a *genealogical* one, nor ever doubts that "*The fact that we are able to classify organisms at all in accordance with the structural characteristics which they present is due to the fact of their being related by descent†.*" But this great and valuable and even fundamental generalisation sometimes carries us too far. It may be safe and sure and helpful and illuminating when we apply it to such complex entities—such thousand-fold resultants of the combination and permutation of many variable characters—as a horse, a lion or an eagle; but (to my mind) it has a very different look, and a far less firm foundation, when we attempt to extend it to minute organisms whose specific characters are few and simple, whose simplicity

* Cf. Bergson, *Creative Evolution*, p. 107: "Certain Foraminifera have not varied since the Silurian epoch. Unmoved witnesses of the innumerable revolutions that have upheaved our planet, the Lingulae are today what they were at the remotest times of the palaeozoic era."

† Ray Lankester, *A.M.N.H.* (4), xi, p. 321, 1873.

becomes more manifest from the point of view of physical and mathematical analysis, and whose form is referable, or largely referable, to the direct action of a physical force. When we come to the minute skeletons of the Radiolaria we shall again find ourselves dealing with endless modifications of form, in which it becomes more and more difficult to discern, and at last vain and hopeless to apply, the guiding principle of affiliation or "phylogeny."

Among the Foraminifera we have an immense variety of forms, which, in the light of surface-tension and of the principle of minimal area, are capable of explanation and of reduction to a small number of characteristic types. Many of them are composite structures, formed by the successive imposition of cell upon cell, and these we shall deal with later on; let us glance here at the simpler conformations exhibited by the single chambered or "monothalamic" genera, and perhaps one or two of the simplest composites.

We begin with forms like *Astrorhiza* (Fig. 320, p. 703), which are large, coarse and highly irregular, and end with others which are minute and delicate, and which manifest a perfect and mathematical regularity. The broad difference between these two types is that the former are characterised, like *Amoeba*, by a variable surface-tension, and consequently by unstable equilibrium; but the strong contrast between these and the regular forms is bridged over by various transition-stages, or differences of degree. Indeed, as in all other Rhizopods, the very fact of the emission of pseudopodia, which are especially characteristic of this group of animals, is a sign of unstable surface-equilibrium; and we must therefore consider, or may at least suspect, that those forms whose shells indicate the most perfect symmetry and equilibrium have secreted these during periods when rest and uniformity of surface-conditions contrasted with the phases of pseudopodial activity. The irregular forms are in almost all cases arenaceous, that is to say they have no solid shells formed by steady adsorptive secretion, but only a looser covering of sand grains with which the protoplasmic body has come in contact and cohered. Sometimes, as in *Ramulina*, we have a calcareous shell combined with irregularity of form; but here we can easily see a partial and as it were a broken regularity, the regular forms of sphere and cylinder being repeated in various

parts of the ramified mass. When we look more closely at the arenaceous forms, we find the same thing true of them; they represent, in whole or part, approximations to the surfaces of equilibrium, spheres, cylinders and so forth. In *Aschemonella* we have a precise replica of the calcareous *Ramulina*; and in *Astrorhiza* itself, in the forms distinguished by naturalists as *A. crassatina*, what is described as the "subsegmented interior*" seems to shew

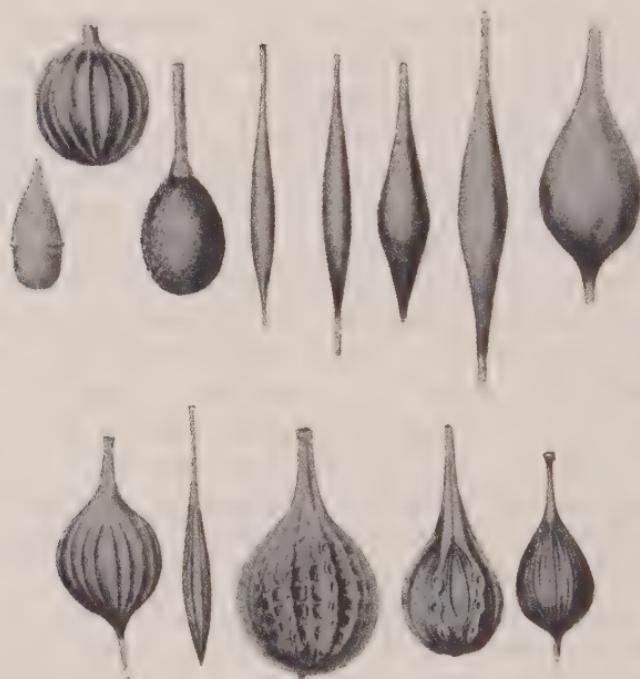


Fig. 130. Various species of *Lagena*. After Brady.

the natural, physical tendency of the long semifluid cylinder of protoplasm to contract at its limit of stability into unduloid constrictions, as a step towards the breaking up into separate spheres: the completion of which process is restrained or prevented by contact with the unyielding arenaceous covering.

Passing to the typical calcareous Foraminifera, we have the most symmetrical of all possible types in the perfect sphere of *Orbulina*; this is a pelagic organism, whose floating habitat gives it a field of

* Brady, *Challenger Monograph*, pl. xx, p. 233.

force of perfect symmetry. Save for one or two other forms which are also spherical, or approximately so, like *Thurammina*, the rest of the monothalamic calcareous Foraminifera are all comprised by naturalists within the genus *Lagena*. This large and varied genus consists of "flask-shaped" shells, whose surface is that of an unduloid, or, like that of a flask itself, an unduloid combined with a portion of a sphere. We do not know the circumstances under which the shell of *Lagena* is formed, nor the nature of the force by which, during its formation, the surface is stretched out into the unduloid form; but we may be pretty sure that it is suspended vertically in the sea, that is to say in a position of symmetry as regards its vertical axis, about which the unduloid surface of revolution is symmetrically formed. types of the same shell in which the form is more or less flattened; and these are doubtless the cases in which such symmetry of position was not present, or was replaced by a broader, lateral contact with the surface pellicle*.

While *Orbulina* is a simple spherical drop, *Lagena* suggests to our minds a hanging drop, drawn out to a longer or shorter neck by

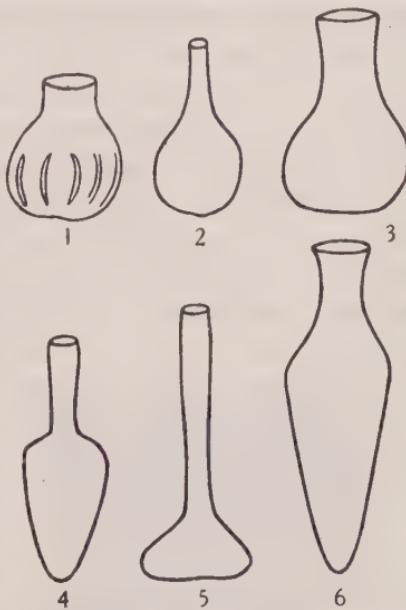


Fig. 131. Roman pottery, for comparison with species of *Lagena*. E.g., 1, 2, with *L. sulcata*; 3, *L. orbigniana*; 4, *L. striata*; 5, *L. crenata*; 6, *L. stelligera*.

At the same time we have other types of the same shell in which the form is more or less flattened; and these are doubtless the cases in which such symmetry of position was not present, or was replaced by a broader, lateral contact with the surface pellicle*.

* That the Foraminifera not only can but do hang from the surface of the water is confirmed by the following apt quotation which I owe to Mr E. Heron-Allen: "Quand on place, comme il a été dit, le dépôt provenant du lavage des fucus dans un flacon que l'on remplit de nouvelle eau, on voit au bout d'une heure environ les animaux [*Gromia dujardinii*] se mettre en mouvement et commencer à grimper. Six heures après ils tapissent l'extérieur du flacon, de sorte que les plus élevés sont à trente-six ou quarante-deux millimètres du fond; le lendemain beaucoup d'entre eux, après avoir atteint le niveau du liquide, ont continué à ramper à sa surface, en se laissant pendre au-dessous comme certains mollusques gastéropodes." (F. Dujardin, *Observations nouvelles sur les prétendus céphalopodes microscopiques*, *Ann. des Sci. Nat.* (2), III, p. 312, 1835.)

its own weight, aided by the viscosity of the material. Indeed the various hanging drops, such as Mr C. R. Darling shews us, are the most beautiful and perfect unduloids, with spherical ends, that it is possible to conceive. A suitable liquid, a little denser than water and incapable of mixing with it (such as ethyl benzoate), is poured on a surface of water. It spreads over the surface and gradually forms a hanging drop, approximately hemispherical; but as more liquid is added the drop sinks or rather stretches downwards, still adhering to the surface film; and the balance of forces between gravity and surface-tension results in the unduloid contour, as the increasing weight of the drop tends to stretch it out and finally break it in two. At the moment of rupture, by the way, a tiny

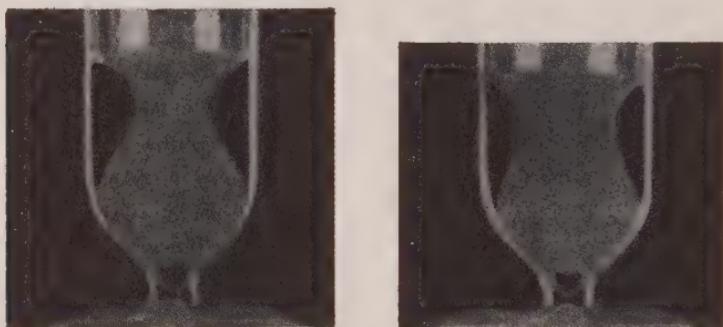


Fig. 132. Large "hanging drops" of oil. After Darling.

droplet is formed in the attenuated neck, such as we described in the normal division of a cylindrical thread.

The thin, fusiform, pointed, non-globular *Lagenas* are less easily explained. Surface-tension, which tends to keep the drop spherical, is overmastered here, and the elongate shape suggests the viscous drag of a shearing fluid*.

To pass to a more highly organised class of animals, we find the unduloid beautifully exemplified in the little flask-shaped shells of certain Pteropod mollusca, e.g. *Cuvierina*†. Here again the symmetry of the figure would at once lead us to suspect that the creature lived in a position of symmetry to the surrounding forces, as for instance if it floated in the ocean in an erect position, that is to say with its long axis coincident with the direction of gravity; and this we know to be actually the mode of life of the little Pteropod.

* Cf. G. I. Taylor, The formation of emulsions in definable fields of flow, *Proc. R.S. (A)*, No. 858, p. 501, 1934.

† Cf. Boas, *Spolia Atlantica*, 1886, pl. 6.

Many species of *Lagena* are complicated and beautified by a pattern, and some by the superaddition to the shell of plane extensions or "wings." These latter give a secondary, bilateral symmetry to the little shell, and are strongly suggestive of a phase or period of growth in which it lay horizontally on the surface, instead of hanging vertically from the surface-film: in which, that is to say, it was a floating and not a hanging drop. The pattern is of two kinds. Sometimes it consists of a sort of fine reticulation, with rounded or more or less hexagonal interspaces: in other cases it is produced by a symmetrical series of ridges or folds, usually longitudinal, on the body of the flask-shaped cell, but occasionally transversely arranged upon the narrow neck. The reticulated and folded patterns we may consider separately. The netted pattern is very similar to the wrinkled surface of a dried pea, or to the more regular wrinkled patterns on poppy and other seeds and even pollen-grains. If a spherical body after developing a "skin" begin to shrink a little, and if the skin have so far lost its elasticity as to be unable to keep pace with the shrinkage of the inner mass, it will tend to fold or wrinkle; and if the shrinkage be uniform, and the elasticity and flexibility of the skin be also uniform, then the amount of foldings will be uniformly distributed over the surface. Little elevations and depressions will appear, regularly interspaced, and separated by concave or convex folds. These being of equal size (unless the system be otherwise perturbed), each one will tend to be surrounded by six others; and when the process has reached its limit, the intermediate boundary-walls, or folds, will be found converted into a more or less regular pattern of hexagons. To these symmetrical wrinkles or shrinkage-patterns we shall return again.

But the analogy of the mechanical wrinkling of the coat of a seed is but a rough and distant one; for we are dealing with molecular rather than with mechanical forces. In one of Darling's experiments, a little heavy tar-oil is dropped on to a saucer of water, over which it spreads in a thin film shewing beautiful interference colours after the fashion of those of a soap-bubble. Presently tiny holes appear in the film, which gradually increase in size till they form a cellular pattern or honeycomb, the oil gathering together in the meshes or walls of the cellular net. Some action of this sort is in all probability at work in a surface-film

of protoplasm covering the shell. As a physical phenomenon the actions involved are by no means fully understood, but surface-tension, diffusion and cohesion play their respective parts therein*. The very perfect cellular patterns obtained by Leduc (to which we shall have occasion to refer in a subsequent chapter) are diffusion patterns on a larger scale, but not essentially different.

The folded or pleated pattern is doubtless to be explained, in a general way, by the shrinkage of a surface-film under certain conditions of viscous or frictional restraint.



Fig. 133.

A case which (as it seems to me) is closely allied to that of our foraminiferal shells is described by Quincke†, who let a film of chromatised gelatin or of resin set and harden upon a surface of quicksilver, and found that the little solid pellicle had been thrown into a pattern of symmetrical folds, as fine as a diffraction grating. If the surface thus folded

or wrinkled be a cylinder, or any other figure with one principal axis

* This cellular pattern would seem to be related to the "cohesion figures" described by Tomlinson in various surface-films (*Phil. Mag.* 1861–70); to the "tesselated structure" on liquid surfaces described by James Thomson in 1882 (*Collected Papers*, p. 136); and (more remotely) to the *tourbillons cellulaires* of Bénard, *Ann. de Chimie* (7), xxiii, pp. 62–144, 1901; (8), xxiv, pp. 563–566, 1911, *Rev. génér. des Sci.* xi, p. 1268, 1900; cf. also E. H. Weber, *Mikroskopische Beobachtungen sehr gesetzmässiger Bewegungen welche die Bildung von Niederschlägen harziger Körper aus Weingeist begleiten*, *Poggend. Ann.* xciv, pp. 447–459, 1855; etc. Some at least of Tomlinson's cohesion-figures arise, according to van Mensbrugghe, from the disengagement of minute bubbles of gas, when a fluid holding gases in solution comes in contact with a fluid of lower surface-tension. The whole phenomenon is of great interest and various appearances have been referred to it, in biology, geology, metallurgy and even astronomy: for the flocculent clouds in the solar photosphere shew an analogous configuration. (See letters by Kerr Grant, Larmor, Wager and others, in *Nature*, April 16 to June 11, 1914; also Rayleigh, *Phil. Mag.* xxxii, p. 529, 1916; G. T. Walker, *Clouds, natural and artificial*, *Royal Inst.* 8 Feb. 1935; etc.) In many instances, marked by strict symmetry or regularity, it is very possible that the interference of waves or ripples may play its part in the phenomenon. But in the majority of cases, it is fairly certain that localised centres of action, or of diminished tension, are present, such as might be provided by dust-particles in the case of Bénard's experiment (cf. *infra*, p. 503).

† Quincke, Ueber physikalische Eigenschaften dünner fester Lamellen, *Sitzungsber. Berlin. Akad.* 1888, p. 789; Ueber ansichtbare Eigenschaften, etc., *Ann. d. Physik*, 1920, p. 653. Quincke found that "sehr kleine Menge fremder Substanz haben eine grosse Einfluss auf die Bildung der Schaumwände."

of symmetry, such as an ellipsoid or unduloid, the folds will tend to be related to the axis of symmetry, and we may expect accordingly to find regular longitudinal, or regular transverse wrinkling. Now as a matter of fact we almost invariably find in *Lagena* the former condition: that is to say, in our ellipsoid or unduloid shell, the puckering takes the form of the vertical fluting on a column, rather than that of the transverse pleating of an accordion; and further, there is often a tendency for such longitudinal flutings to be more or less localised at the end of the ellipsoid, or in the region where the unduloid merges into its spherical base*. In the latter region we often meet with a regular series of short longitudinal folds, as in the forms denominated *L. semistriata*. All these various forms of surface can be imitated, or precisely reproduced, by the art of the glass-blower; and they can be seen in a contracting bubble of saponin, though not in the more fluid soap-bubble. They remind one of the ribs or flutings in the film or sheath which splashes up to envelop a smooth pebble dropped into a liquid, as Mr Worthington has so beautifully shewn.

In Mr Worthington's experiment there appears to be something of the nature of a viscous drag in the surface-pellicle; but whatever be the actual cause of variation of tension, it is not difficult to see that there must be in general a tendency towards *longitudinal* puckering or "fluting" in the case of a thin-walled cylindrical or other elongated body, rather than a tendency towards transverse puckering, or "pleating." For let us suppose that some change takes place involving an increase of surface-tension in some small area of the curved wall, and leading therefore to an increase of pressure: that is to say let T become $T + t$, and P become $P + p$. Our new equation of equilibrium, then, in place of $P = T/r + T/r'$, becomes

$$P + p = \frac{T + t}{r} + \frac{T + t}{r'},$$

* Certain palaeontologists (e.g. Haeusler and Spandl) have asserted that in each family or genus the plain smooth-shelled forms are primitive and ancient, and that the ribbed and otherwise ornamented shells make their appearance at later dates in the course of advancing evolution (cf. Rhumbler, *Foraminiferen der Plankton-Expedition*, 1911, p. 21). If this were true it would be of fundamental importance: but this book of mine would not deserve to be written.

and by subtraction,

$$p = t/r + t/r'.$$

Now if

$$r < r', \quad t/r > t/r'.$$

Therefore, in order to produce the small increment of pressure p , it is easier to do so by increasing t/r than t/r' ; that is to say, the easier way is to alter or diminish r . And the same will hold good if the tension and pressure be diminished instead of increased.

This is as much as to say that, when corrugation or "rippling" of the walls takes place owing to small changes of surface-tension, and consequently of pressure, such corrugation is more likely to take place in the plane of r —that is to say, *in the plane of greatest curvature*. And it follows that in such a figure as an ellipsoid, wrinkling will be most likely to take place not only in a longitudinal direction but near the extremities of the figure, that is to say again in the region of greatest curvature.

The longitudinal wrinkling of the flask-shaped bodies of our *Lagenae*, and of the more or less cylindrical cells of many other Foraminifera (Fig. 134), is in complete accord with the above considerations; but nevertheless, we soon find that our result is not a general one but is defined by certain limiting conditions, and is accordingly subject to what are, at first sight, important exceptions. For instance, when we turn to the narrow neck of the *Lagena* we see at once that our theory no longer holds; for the wrinkling which was invariably longitudinal in the body of the cell is as invariably transverse in the narrow neck. The reason for the difference is not far to seek. The conditions in the neck are very different from those in the expanded portion of the cell: the main difference being that the thickness of the wall is no longer insignificant, but is of considerable magnitude as compared with the diameter, or circumference, of the neck. We must accordingly take it into account in considering the *bending moments* at any point in this region of the shell-wall. And it is at once obvious that, in any portion of the narrow neck, *flexure* of a wall in a transverse direction will be very difficult, while flexure in a longitudinal direction will be comparatively easy; just as, in the case of a long narrow strip of iron, we may easily bend it into folds running transversely to its long axis, but not the other way. The manner in which our little *Lagena*-shell

tends to fold or wrinkle, longitudinally in its wider part and transversely or annularly in its narrow neck, is thus completely explained.

An identical phenomenon is apt to occur in the little flask-shaped gonangia, or reproductive capsules, of some of the hydroid zoophytes. In the annexed drawings of these gonangia in two species of *Campanularia*, we see that in one case the little vesicle has the flask-shaped or unduloid configuration of a *Lagena*; and here the walls of the flask are longitudinally fluted, just after the manner we have witnessed in the latter genus. In the other Campanularian the vesicles are long, narrow and tubular, and here a transverse folding



Fig. 134. *Nodosaria scalaris*
Batsch.



Fig. 135. Gonangia of Campanularians.
(a) *C. gracilis*; (b) *C. grandis*.
After Allman.



or pleating takes the place of the longitudinally fluted pattern; and the very form of the folds or pleats is enough to suggest that we are not dealing here with a simple phenomenon of surface-tension, but with a condition in which surface-tension and stiffness are both present, and play their parts in the resultant form.

An everted rim, or short neck, may arise in various ways apart from the phenomenon of the hanging drop. To make a "thistle-head" the glassblower blows a bubble, and from that another one; after blowing the latter up large and thin he crushes it to pieces, and melting down what is left of it he forms the rim. I take it that the neck or rim of the shell in *Diffugia* is formed in an analogous way, in connection with the growth of a new individual at the mouth

of the first. There is a very neat expanded orifice in the cyst of *Chromulina* (Fig. 136); it is doubtless fashioned in just as simple a way, but how I know not.

Passing from the solitary flask-shaped cell of *Lagena*, but without leaving the Foraminifera, we find in *Nodosaria*, *Rheophax* or *Sagrina* constricted cylinders, or successive unduloids, such as are represented in Fig. 137. In some of these, as in the arenaceous genus



Fig. 136. Flask-shaped shells or cysts. *a, b, Chromulina* and *Deropyxis* (Flagellata); *c, Diffugia*.



Fig. 137. Various species of *Nodosaria*, *Rheophax*, *Sagrina*. After Brady.

Rheophax, we have to do with the ordinary phenomenon of a partially segmenting cylinder. But in others, the structure is not developed out of a continuous protoplasmic cylinder, but, as we can see by examining the interior of the shell, it has been formed in successive stages, beginning with a simple unduloid "*Lagena*," about which, after it solidified, another drop of protoplasm accumulated, and in turn assumed the unduloid or lagenoid form. The chains of interconnected bubbles which Morey and Draper made many years ago of melted resin are a similar if not identical phenomenon*.

* See *Silliman's Journal*, II, p. 179, 1820; and cf. Plateau, *op. cit.* II, pp. 134, 461.

Fishes shew a vast though limited variety of form; and some of the strangest shapes are found in the great depths of the ocean. Here, in unchanging temperature, in darkness save for a few phosphorescent rays, above all in unruffled stillness and eternal

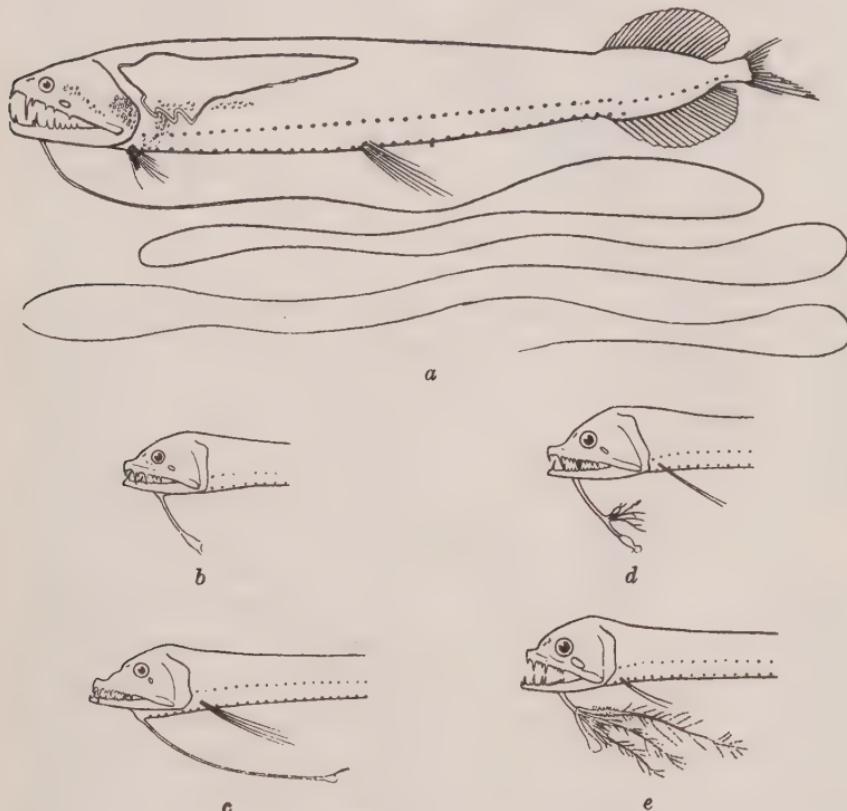


Fig. 138. Deep-sea fishes (Stomiataidae). *a*, *Lamprotoxus flagellibarbis*; *b*, *Eustomias dactylopus*; *c*, *E. parri*; *d*, *E. schmidti*; *e*, *E. silvescens*. * After Tate Regan and Trewavas.

calm*, the conditions of life are strange indeed. In deep-sea fishes length and attenuation are common characters of the body and of its parts. A barbel below the lip may grow to ten times the whole length of the fish; it ends, commonly, in a little bulb or blob; it may give off threadlike branches, and these last slender filaments

* In Overbeck's jet-experiments (*supra*, p. 394) the water into which the jet is led must first stand for many hours, till all internal movements and temperature-differences are eliminated.

are sometimes finely beaded*; and slight differences in the beading and branching are said to characterise allied species of fish. Such a barbel looks like a jet or branching stream of one fluid falling

through another. It may indeed be that in these quiet depths growth easily follows its lines of least resistance, and that in the shaping of these peculiar out-growths hydrodynamical and capillary forces are taking the upper hand.

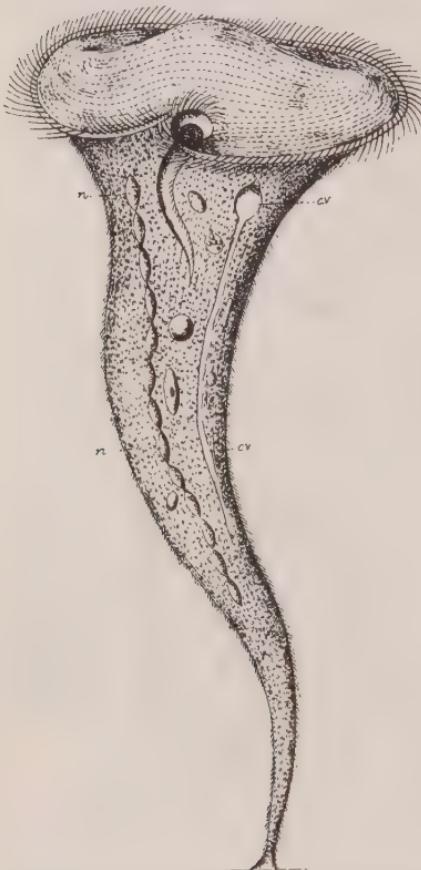


Fig. 139. *Stentor*, a ciliate infusorian: from Savile Kent.

of which we have not so far found a physical analogue. Here the curved contour seems to enter, re-enter, and disappear within the substance of the body, so bounding a deep and twisted space or passage, which merges with the fluid contents and vanishes within the cell, and is called by naturalists the "gullet." This very peculiar and complicated structure is only kept in equilibrium, and in existence, by the constant activity of cilia over the general surface

* See, for instance, C. Tate Regan and E. Trewavas on *The Stomiatiidae of the Dana Expedition*, 1930; W. Beebe, Deep-sea Stomiatioids, *Copeia*, Dec. 1833.

of the body and very especially in the said gullet or re-entrant portion of the surface. Now we have seen the nodoid to be a curved surface, re-entering on itself and endless; no method of support, by wire-rings or otherwise, enables us to construct or realise more than a small portion of it. But the typical ciliate, such as *Paramecium*, looks just like what we might expect a nodoid surface to be, if we could only realise it (or a single segment of it) in a drop of fluid, and imagine it to be kept in quasi-equilibrium by continual ciliary activity. I suspect, indeed, that here is nothing more, and nothing less, than a partial realisation of the nodoid itself; that the so-called gullet is but the characteristic inversion or "kink" in that curve; and that the cilia, which normally clothe the surface and always line the gullet, are needed to realise and to maintain the unstable equilibrium of the figure. If this be so—it is a suggestion and no more—we shall have found among our simple organisms the complete realisation, in varying abundance, of each and all of the six surfaces of Plateau. On each and all of them we have a host of beautiful "patterns" of various sorts; all of them so beautiful and so symmetrical that they *ought* to be capable of geometric representation—and all waiting for their interpreter!

From all these configurations, which the law of minimal area controls and dominates, *Amoeba* stands aloof and alone. The rest are all figures of equilibrium, unstable though it may sometimes be. But *Amoeba* is the characteristic case of a fluid surface without an equilibrium; it is the very negation of stability. In composition it is neither constant nor homogeneous; its chemistry is in constant flux, its surface energies vary from here to there, its fluid substance is drawn hither and thither; within and without it is never still, be its motions swift or be they slow. The heterogeneity of its system points towards a maximal surface-area, rather than a minimal one; only here and there, in small portions of its heterogeneous substance, do we see the rounded contours of a fluid drop, in token of temporary equilibrium. Only when its heterogeneous reactions quieten down and the little living speck enters on its "resting-stage," does the protoplasmic body withdraw itself into a sphere and the law of area minima come into its own. Physically analogous is the case of such complicated pseudopodia, or "axopodia", as we find among the Foraminifera and Heliozoa: where the whole

fabric is in a flux, and currents flow and granules are carried hither and thither. Here again there is no statical equilibrium; but surface tension varies, as does the chemistry of the protoplasm, from one spot to another.

The great oceanic group of the Radiolaria, and the highly complicated skeletons which they construct, give us many beautiful illustrations of physical phenomena, among which the effects of surface-tension are as usual prominent. But we shall deal later on with these little skeletons under the head of spicular concretions.

In a simple and typical Heliozoan, such as the sun-animalcule, *Actinophrys sol*, we have a "drop" of protoplasm, contracted by its surface tension into a spherical form. Within this heterogeneous protoplasm are more fluid portions, and a similar surface-tension causes these also to assume the form of spherical "vacuoles," or of little clear drops within the big one; unless indeed they become numerous and closely packed, in which case they run together and constitute a "froth," such as we shall study in the next chapter. One or more of such clear spaces may be what is called a "contractile vacuole": that is to say, a droplet whose surface-tension is in unstable equilibrium and is apt to vanish altogether, so that the definite outline of the vacuole suddenly disappears*. Again, within the protoplasm are one or more nuclei, whose own surface-tension draws them in turn into the shape of spheres. Outwards through the protoplasm, and stretching far beyond the spherical surface of the cell, run stiff linear threads of modified protoplasm, reinforced in some cases by delicate siliceous needles. In either case we know little or nothing about the forces which lead to their production, and we do not hide our ignorance when we ascribe their development to a "radial polarisation" of the cell. In the case of the protoplasmic filament, we may (if we seek for a hypothesis) suppose that it is somehow comparable to a viscid stream, or "liquid vein," thrust or spirited out from the body of the cell. But when it is once formed, this long and comparatively rigid filament is separated by a distinct surface from the neighbouring

* The presence or absence of the contractile vacuole or vacuoles is one of the chief distinctions, in systematic zoology, between the Heliozoa and the Radiolaria. As we have seen on p. 295 (footnote), it is probably no more than a physical consequence of the different conditions of existence in fresh and in salt water.

protoplasm, that is to say, from the more fluid surface-protoplasm of the cell; and the latter begins to creep up the filament, just as water would creep up the interior of a glass tube, or the sides of a glass rod immersed in the liquid. It is the simple case of a balance between three separate tensions: (1) that between the filament and the adjacent protoplasm, (2) that between the filament and the adjacent water, and (3) that between the water and the protoplasm. Calling these tensions respectively T_{fp} , T_{fw} , and T_{wp} , equilibrium will be attained when the angle of contact between the fluid

protoplasm and the filament is such that $\cos \alpha = \frac{T_{fw} - T_{wp}}{T_{fp}}$. It is

evident in this case that the angle is a very small one. The precise form of the curve is somewhat different from that which, under ordinary circumstances, is assumed by a liquid which creeps up a solid surface, as water in contact with air creeps up a surface of glass; the difference being due to the fact that here, owing to the density of the protoplasm being all but identical with that of the surrounding medium, the whole system is practically immune from gravity. Under normal circumstances the curve is part of the "elastic curve" by which that surface of revolution is generated which we have called, after Plateau, the nodoid; but in the present case it is apparently a catenary. Whatever curve it be, it obviously forms a surface of revolution around the filament.

Since this surface-tension is symmetrical around the filament, the latter will be pulled equally in all directions; in other words the filament will tend to be set normally to the surface of the sphere, that is to say radiating directly outwards from the centre. If the distance between two adjacent filaments be considerable, the curve will simply meet the filament at the angle α already referred to; but if they be sufficiently near together, we shall have a continuous catenary curve forming a hanging loop between one filament and the other. And when this is so, and the radial filaments are more or less symmetrically interspaced, we may have a beautiful system of honeycomb-like depressions over the surface of the organism, each cell of the honeycomb having a strictly defined geometric configuration (cf. p. 710).

In the simpler Radiolaria, the spherical form of the entire organism is equally well marked; and here, as also in the more complicated

Heliozoa (such as *Actinosphaerium*), the organism is apt to be differentiated into layers, so constituting sphere within sphere, whose inter-surfaces become the seat of adsorption, and the locus of skeletal secretion. One layer at least is close-packed with vacuoles, forming an "alveolar meshwork," with the configurations of which we shall attempt in another chapter to correlate certain characteristic types of skeleton. In *Actinosphaerium* the radial filaments pass through the outer layer, and seem to rest on but do not penetrate the layer below; this must happen if the surface-energy between the one plasma-layer and the other be less than that between the filament and the water around*.

A very curious conformation is that of the vibratile "collar," found in *Codosiga* and the other "Choanoflagellates," and which we also meet with in the "collar-cells" which line the interior cavities of a sponge. Such collar-cells are always very minute, and the collar is constituted of a very delicate film which shews an undulatory or rippling motion. It is a surface of revolution, and as it maintains itself in equilibrium (though a somewhat unstable and fluctuating one) it must be, under the restraining circumstances of its case, a surface of minimal area. But it is not so easy to see what these special circumstances are, and it is obvious that the collar, if left to itself, must shrink or shrivel towards its base and become confluent with the general surface of the cell; for it has no longitudinal supports and no strengthening ring at its periphery. But in all these collar-cells, there stands within the annulus of the collar a large and powerful cilium or flagellum, in constant movement; and by the action of this flagellum, and doubtless in part also by the intrinsic vibrations of the collar itself, there is set up a constant steady current in the surrounding water, whose direction would seem to be such that it passes up the outside of the collar, down its inner side, and out in the middle in the direction of the flagellum; and there is a distinct eddy, in which foreign particles tend to be caught, around the peripheral margin of the collar†.

* Cf. N. K. Koltzoff, *Anat. Anzeiger*, xli, p. 190, 1912.

† The very minute size of *Codosiga*, whose collar and flagellum measure about 30–40 μ , and of all such collar-cells, make the apparently complex current-system all the harder to comprehend. Cf. G. Lepage, Notes on *C. botrytis*, *Q.J.M.S.* LXIX, pp. 471–508, 1925

When the cell dies, that is to say when motion ceases, the collar immediately shrivels away and disappears. It is notable, by the way, that the edge of this little mobile cup is always smooth, never notched or lobed as in the cases we have discussed on p. 390: this latter condition being the outcome of a definite instability, marking the close of a period of equilibrium. But the vibratile collar of *Codosiga* is in "a steady state," its equilibrium, such as it is, being constantly renewed and perpetuated, like that of a juggler's pole, by the motions of the system. Somehow its existence is due to the current motions and to the traction exerted upon it through the friction of the stream which is constantly passing by. In short, I think that it is formed very much in the same way as the cup-like ring of streaming ribbons, which we see fluttering and vibrating in the air-current of a ventilating fan. If we turn once more to Mr Worthington's *Study of Splashes*, we may find a curious suggestion of analogy in the beautiful craters encircling a central jet (as the collar of *Codosiga* encircles the flagellum), which we see produced in the later stages of the splash of a pebble.

Another exceptional form of cell, and beautiful manifestation of capillarity, occurs in Trypanosomes, those tiny parasites of the blood which are associated with sleeping-sickness and certain other dire maladies of beast and man. These minute organisms consist of elongated solitary cells down one side of which runs a very delicate frill, or "undulating membrane," the free edge of which is seen to be slightly thickened, and the whole of which undergoes rhythmical and beautiful wavy movements. When certain Trypanosomes are artificially cultivated (for instance *T. rotatorium*, from the blood of the frog), phases of growth are witnessed in which the organism has no undulating membrane, but possesses a long cilium or "flagellum," springing from near the front end, and exceeding the whole body in length*. Again, in *T. lewisi*, when it reproduces by "multiple fission," the products of this division are likewise

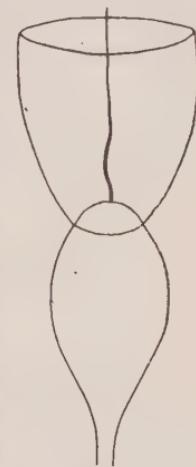


Fig. 140.

* Cf. Doflein, *Lehrbuch der Protozoenkunde*, 1911, p. 422.

devoid of an undulating membrane, but are provided with a long free flagellum*. It is a plausible assumption to suppose that, as the flagellum waves about, it comes to lie near and parallel to the body of the cell, and that the frill or undulating membrane is formed by the clear, fluid protoplasm of the surface layer springing up in

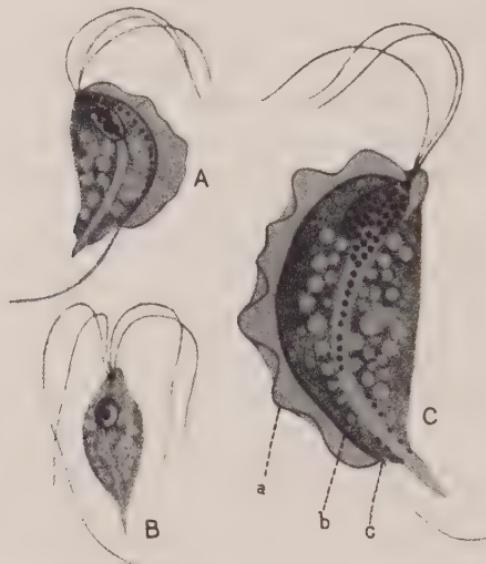


Fig. 141. *A*, *Trichomonas muris* Hartmann; *B*, *Trickomastix serpentis* Dobell; *C*, *Trichomonas angusta* Alexeieff. After Kofoid.



Fig. 142. A Trypanosome.

a film to run up and along the flagellum, just as a soap-film would form under similar circumstances.

This mode of formation of the undulating membrane or frill appears to be confirmed by the appearances shewn in Fig. 141. Here we have three little organisms closely allied to the ordinary Trypanosomes, of which one, *Trickomastix* (*B*), possesses four flagella, and the other two, *Trichomonas*, apparently three only:

* Cf. Minchin, *Introduction to the Study of the Protozoa*, 1914, p. 293, Fig. 127.

the two latter possess the frill, which is lacking in the first*. But it is impossible to doubt that when the frill is present (as in *A* and *C*), its outer edge is constituted by the apparently missing flagellum *a*, which has become *attached* to the body of the creature at the point *c*, near its posterior end; and all along its course the superficial protoplasm has been drawn out into a film, between the flagellum *a* and the adjacent surface or edge of the body *b*.

Moreover, this mode of formation has been actually witnessed and described, though in a somewhat exceptional case. The little flagellate monad *Herpetomonas* is normally destitute of an undulating membrane, but possesses a single long terminal flagellum. According to Prof. D. L. Mackinnon, the cytoplasm in a certain stage of growth becomes somewhat "sticky," a phrase which we may in all probability interpret to mean that its surface-tension is being reduced. For this stickiness is shewn in two ways. In the first place, the long body, in the course of its various bending movements, is apt to adhere head to tail (so to speak), giving a rounded or sometimes annular form to the organism, such as has also been described in certain species or stages of Trypanosomes. But again, the long flagellum, if it get bent backwards upon the body, tends to adhere to its surface. "Where the flagellum was pretty long and active, its efforts to continue movement under these abnormal conditions resulted in the gradual lifting up from the cytoplasm of the body of a sort of *pseudo*-undulating membrane (Fig. 143). The movements of this structure were so exactly those of a true undulating membrane that it was difficult to believe one was not dealing with a small, blunt Trypanosome"**: This in short is a precise

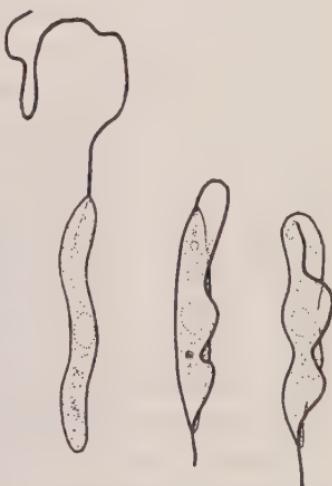


Fig. 143. *Herpetomonas* assuming the undulatory membrane of a Trypanosome. After D. L. Mackinnon.

* Cf. C. A. Kofoid and Olive Swezy, On Trichomonad flagellates, etc., *Pr. Amer. Acad. of Arts and Sci.* LI, pp. 289-378, 1915. Also C. H. Martin and Muriel Robertson, *Q.J.M.S.* LVII, pp. 53-81, 1912.

† D. L. Mackinnon, Herpetomonads from the alimentary tract of certain dungflies, *Parasitology*, III, p. 268, 1910.

description of the mode of development which, from theoretical considerations alone, we should conceive to be the natural if not the only possible way in which the undulating membrane could come into existence.

There is a genus closely allied to *Trypanosoma*, viz. *Trypanoplasma*, which possesses one free flagellum, together with an undulating membrane; and it resembles the neighbouring genus *Bodo*, save that the latter has two flagella and no undulating membrane. In like manner, *Trypanosoma* so closely resembles *Herpetomonas* that, when individuals ascribed to the former genus exhibit a free flagellum only, they are said to be in the "Herpetomonas stage." In short, all through the order, we have pairs of genera which are presumed to be separate and distinct, viz. *Trypanosoma-Herpetomonas*, *Trypanoplasma-Bodo*, *Trichomastix-Trichomonas*, in which one differs from the other mainly if not solely in the fact that a free flagellum in the one is replaced by an undulating membrane in the other. We can scarcely doubt that the two structures are essentially one and the same.

The undulating membrane of a Trypanosome, then, according to our interpretation of it, is a liquid film and must obey the law of constant mean curvature. It is under curious limitations of freedom: for by one border it is attached to the comparatively motionless body, while its free border is constituted by a flagellum which retains its activity and is being constantly thrown, like the lash of a whip, into wavy curves. It follows that the membrane, for every alteration of its longitudinal curvature, must at the same instant become curved in a direction perpendicular thereto; it bends, not as a tape bends, but with the accompaniment of beautiful but tiny waves of double curvature, all tending towards the establishment of an "equipotential surface", which indeed, as it is under no pressure on either side, is really a surface of no curvature at all; and its characteristic undulations are not originated by an active mobility of the membrane but are due to the molecular tensions which produce the very same result in a soap-film under similar circumstances. Some of the larger Spirochaetes possess a structure so like to the undulating membrane of the Trypanosomes that it has led some persons to include these peculiar allies of the bacteria among the flagellate protozoa; but it would seem (according to the weight of

evidence) that the Spirochaete membrane does not undulate, and possesses no thickened border or marginal filament (*Randfade*)*. It forms a "screw-surface," or helicoid, and, though we might think that nothing could well be more curved, yet its mathematical properties are such that it constitutes a "ruled surface" whose mean curvature is everywhere *nil*. Precisely such a surface, and of exquisite beauty, may be produced by bending a wire upon itself so that part forms an axial rod and part winds spirally round the axis, and then dipping the whole into a soapy solution.



Fig. 144. *Dinenymphpha gracilis* Leidy.

A peculiar type is the flattened spiral of *Dinenymphpha*†, which reminds us of the cylindrical spiral of a *Spirillum* among the bacteria. Here we have a symmetrical figure, whose two opposite surfaces each constitute a surface of constant mean curvature; it is evidently

* For a discussion of this obscure lamella, and of the *crista* which seems to correspond with it in other species, see Doflein, *Probleme der Protistenkunde*, II, Die Natur der Spirochaeten, Jena, 1911; see also Clifford Dobell, *Arch. f. Protistenkunde*, 1912.

† Leidy, Parasites of the termites, *Journ. Nat. Sci., Philadelphia*, VIII, pp. 425-447, 1874-81; cf. Savile-Kent's *Infusoria*, II, p. 551.

a figure of equilibrium under certain special conditions of restraint. The cylindrical coil of the *Spirillum*, on the other hand, is a surface of constant mean curvature, and therefore of equilibrium, as truly, and in the same sense, as the cylinder itself.

A very beautiful "saddle-shaped" surface, of constant mean curvature, is to be found in the little diatom *Campylodiscus*, and others, a little more complicated, in the allied genus *Surirella**.

These undulating and helicoid surfaces are exactly reproduced among certain forms of spermatozoa. The tail of a spermatozoon consists normally of an axis surrounded by clearer and more fluid protoplasm, and the axis sometimes splits up into two or more slender filaments. To surface-tension operating between these and the surface of the fluid protoplasm (just as in the case of the flagellum of the Trypanosome), I ascribe the formation of the undulating membrane which we find, for instance, in the spermatozoa of the newt or salamander; and of the helicoid membrane, wrapped in a far closer and more beautiful spiral than that which we saw in Spirochaeta, which is characteristic of the spermatozoa of many birds. The undulatory membrane which certain *ciliate* infusoria exhibit is, seemingly, a different thing. It is not based on a single marginal flagellum, but consists of a row of fine cilia fused together. The membrane can be broken up by certain reagents into fibrillae, and—what is more remarkable—a touch of the micro-dissection needle may split it into a multitude of cilia, all active but beating out of time; a moment more and they unite again, all but disappearing from view as they fuse into the optically homogeneous membrane. They unite as quickly and as intimately as though they were so many liquid jets, and they manifestly "partake of fluidity." Neither they, nor cilia in general, have received, nor seem likely to receive, a simple explanation†. Nevertheless, we may see a little light in the darkness after all.

It would be overbold to seek for every form of living cell a parallel configuration due to simple capillary forces, as manifested in drop or bubble or jet. And yet, if the simple cases of sphere or cylinder be the beginning of the story, they assuredly are not the end. The

* Van Heurck, *Synopsis des Diatomées de Belgique*, pls. lxxiv, 6; lxxvii, 4.

† H. N. Maier, Der feinere Bau der Wimpernapparate der Infusorien, *Arch. f. Protistenk.* II, p. 73, 1903; R. Chambers and J. A. Dawson, Structure of the undulating membrane in the ciliate *Blepharisma*, *Biol. Bull.* XLVIII, p. 240, 1925.

pointed and flagellate cell of a *Monad*, one of the least and commonest of micro-organisms, is far removed from a simple "drop," and all its characters, to the microscopist's eye, are both generally and specifically those of a living thing. But a drop of water falling through an electric field, as in a thunderstorm, is found to lengthen out to three or four times as long as it is broad; and then, if the strength of the field increase a little, the prolate drop becomes unstable, it grows spindle-shaped, and suddenly from one of its two pointed spindle-ends (the positive end especially) a long and slender filament shoots out, to the accompaniment of an electrical discharge. We need not assert that the phenomena are identical, nor that the forces in action are absolutely the same. Yet it is no small thing to have learned that the peculiar conformation of the little flagellate *Monad* has its *analogue* in an electrified drop, and is not unique after all*.

Before we pass from the subject of the conformation of the solitary cell we must take some account of certain other exceptional forms, less easy of explanation, and still less perfectly understood. Such is the case, for instance, of the red blood-corpuscles of man and other vertebrates; and among the sperm-cells of the decapod crustacea we find forms still more aberrant and not less perplexing. These are among the comparatively few cells or cell-like structures whose form *seems* to be incapable of explanation by theories of surface-tension.

In all the mammalia (save a very few) the red blood-corpuscles are flattened circular discs, dimpled in upon their two opposite sides. This configuration closely resembles that of an india-rubber ball when we pinch it tightly between finger and thumb†.

The form of the corpuscle is symmetrical; it is a solid of revolution, but its surface is not a surface of constant mean curvature. From the surface-tension point of view, the blood-corpuscle is not a surface of equilibrium; in other words, it is not a fluid drop poised

* Cf. W. A. Macky, On the deformation of water-drops in strong electric fields, *Proc. R.S. (A)*; cxxxiii, pp. 565-587, 1931.

† On this analogy we might expect the double concavity to pass, with no great difficulty, into the single hollow of a cup or bell, and such a shape the blood-corpuscles are said sometimes to assume. Cf. Weidenreich, *Arch. f. mikr. Anat.* LXVII, 1902; and cf. Clerk-Maxwell on "dimples" in *Tr. R.S.E.* xxvi, p. 11, 1870.

in another liquid. Some other force or forces must be at work to conform it, and the simple effect of mechanical pressure is excluded, because the corpuscle exhibits its characteristic shape while floating freely in the blood. It has been suggested that the corpuscle is perhaps comparable to a solid of revolution described about one of Cayley's equipotential curves*, such as we have spoken of briefly on p. 318. Were the corpuscle a sphere, or a thin plate, a gas diffusing inwards would reach all parts equally soon; but the surface

would be small in the one case and the volume in the other. In so far as the corpuscle resembles or approaches the equipotential form, we might look on it as a compromise; but however advantageous such a shape might be, and

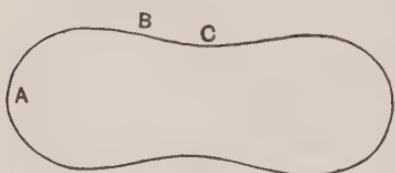


Fig. 145.

however interesting physiologically, we should be as far as ever from understanding how it was produced. In all other vertebrates, from fishes to birds, sluggish or active, warm-blooded or cold, the blood-corpuscles have the simpler form of a flattened oval disc, with somewhat sharp edges and ellipsoidal surfaces, and this again is manifestly not a surface of fluid equilibrium. But there is nothing to choose between the one type and the other in the way of physiological efficiency, nor any apparent need for a refinement of adaptive form in either of them.

Two facts are noteworthy in connection with the form of the mammalian blood-corpuscle. In the first place its form is only maintained, that is to say it is only in equilibrium, in specific relation to the medium in which it floats. If we add water to the blood, the corpuscle becomes a spherical drop, a true surface of minimal area and stable equilibrium; if, conversely, we add a little salt, or a drop of glycerine, the corpuscle shrinks, and its surface becomes puckered and uneven. So far, it merely obeys the laws of diffusion; but the phenomenon is more complex than this†. For the spherical form is assumed just as well in various *isotonic* solutions, leaving

* Cf. H. Hartridge, *Journ. Physiol.* LIII, p. lxxxii, 1919-20; Eric Ponder, *Journ. Gen. Physiol.* IX, pp. 197-204, 625-629, 1925-26.

† Cf. A. Gough, On the assumption of a spherical form by human blood-corpuscles, *Biochem. Journ.* xviii, p. 202, 1924.

the volume unchanged; a little ammonium oxalate impedes or inhibits the change of form, a little serum brings the spherical corpuscles back to biconcave discs again. We are no longer dealing with simple diffusion, but with phenomena of a very subtle kind.

Secondly, the form of the corpuscle can be imitated artificially by means of other colloid substances. Many years ago Norris made the interesting observation that drops of glue in an emulsion assumed a biconcave form closely resembling that of the mammalian corpuscles*; the glue was impure and doubtless contained lecithin. Waymouth Reid made similar emulsions of cholesterol oleate, in which the same conformation of the drops or particles is beautifully shewn; and Emil Hatschek has made somewhat similar biconcave bodies by dropping gelatine containing potassium ferrocyanide into copper sulphate or a tannin solution. Here Hatschek believes that his biconcave drops are half-formed vortex-rings, arrested by the formation of a semi-permeable membrane; but the explanation does not seem to fit the blood-corpuscle. The cholesterol bodies in Waymouth Reid's experiment are such as have a place of their own among Lehmann's "fluid crystals"†; and it becomes at least conceivable that obscure forces akin to those of crystallisation may be playing their part along with surface-energy in these strange but familiar conformations. The case is a hard one in every way. From the physiological point of view it is difficult and complex enough. For the surface of the corpuscle is equivalent to a semi-permeable membrane‡, through which certain substances pass freely but not others—for the most part anions and not cations§; and accordingly we have here in life a steady state of osmotic equilibrium, of negative osmotic tension within, and to this comparatively simple cause the imperfect distension of the corpuscle may be due.

* *Proc. R.S.* xii, pp. 251–257, 1862–63.

† Cf. (*int. al.*) Lehmann, Ueber scheinbar lebende Kristalle und Myelinformen, *Arch. f. Entw. Mech.* xxvi, p. 483, 1908; *Ann. d. Physik*, xliv, p. 969, 1914.

‡ That no "true membrane" exists has long been known; cf. (*int. al.*) Röhring, *Koll. Chem. Beihefte*, viii, pp. 337–398, 1916. On the other hand the surface of the corpuscle is defined by a monolayer, and very probably by the still more stable condition of two "interpenetrating" monolayers, a proteid and a lipoid. Cf. Eric Ponder, *Phys. Rev.* xvi, p. 19, 1936; and on "interpenetration," Schulman and Rideal in *Proc. R.S.* (B), cxxii, pp. 29–57, 1937.

§ Cf. Hamburger, *Z. f. physikal. Chem.* lxix, p. 663, 1909; *Pflüger's Archiv*, 1902, p. 442; etc.

Whatever the forces are which make and keep the man's corpuscle a dimpled disc and the frog's a flattened ellipsoid, they seem to be of a powerful kind. When we submit either to great hydrostatic pressure, it tends to become spherical at last, the natural result of uniform pressure over its whole surface; but the pressure necessary to bring this result about is very great indeed*. Since the form of the blood-corpuscle cannot, then, be rated as a figure of equilibrium, we must be content to regard it as a "steady state"; and this, moreover, is all we can say of its physico-chemical condition. The red blood-corpuscle, especially the non-nucleated one, is in no ordinary sense *alive*†. It has no power of movement, of reproduction or of repair; it is a mere haemoglobin-freighted drop of protein; its own metabolism, apart from its alternate give and take of oxygen, is slight indeed or absent altogether. But all the same, chemical change is continually going on; anions (like HCO_3) pass freely through its walls, simple cations (like Na, K) find it impermeable; and so, between plasma and corpuscles the conditions are fulfilled for that steady osmotic state known as a "Donnan equilibrium." Somehow, but we know not how, a steady state is maintained alike in the corpuscle's osmotic equilibrium and in its form.

In mammalian blood, the running together of the round biconcave corpuscles into "rouleaux" gives a well-known and characteristic picture. When cold, rouleaux are formed slowly, in warmed plasma they form quickly and well, in salt-solution they do not form at all.

* The whole phenomenon would become simple and mechanical if we might postulate a stiffer peripheral region to the corpuscle, in the form (for instance) of an elastic ring. Such an annular stiffening, like the "collapse-rings" which an engineer inserts in a boiler or the whalebone ring which a Breton fisherman fits into his beret, has been repeatedly asserted to exist; by Dehler, *Arch. f. mikr. Anat.* XLVI, 1895; by Meves, *ibid.* LXXVII, 1911; and especially by J. Rünstrom, Was bedingt die Form und die Formveränderungen der Säugetiererythrocyten, *Arch. f. Entw. Mech.* 1, pp. 391–409, 1922. It has been denied at least as often; but the remarkable statement has been lately made that in a corpuscle which has been swollen up and then brought back to its biconcave form, the dimples reappear on the same sides as before: apparently in "strong evidence for some sort of fixed cellular structure"; see R. F. Furchtgott and Eric Ponder in *Journ. Exp. Biol.* XVII, pp. 30–44, 117–127, 1940. See also, on the whole subject, Eric Ponder, *The Mammalian Red Cell*, Berlin, 1934.

† Cf. A. V. Hill, *Trans. Faraday Soc.* xxvi, p. 667, 1930; *Proc. R.S. (B)*, 1930; K. R. Dixon, in *Current Sci.* vii, p. 169, 1938; etc.

The phenomenon, though a purely physical one, is none too clear. There is a difference of electrical potential between corpuscles and plasma, and the charged corpuscles tend to repel one another; but they also tend to adhere together, all the more when they meet broadside on, whether by actual stickiness or through surface-energy. The attractive forces then overcome the repulsive, and the rouleau is formed. But if the potential be reduced, and mutual repulsion reduced with it, then the corpuscles stick together just as they happen to meet; rouleaux are no longer formed, and ordinary "agglutination" takes place. Whatever be the precise nature of the phenomenon, the number of rouleaux and the mean number of

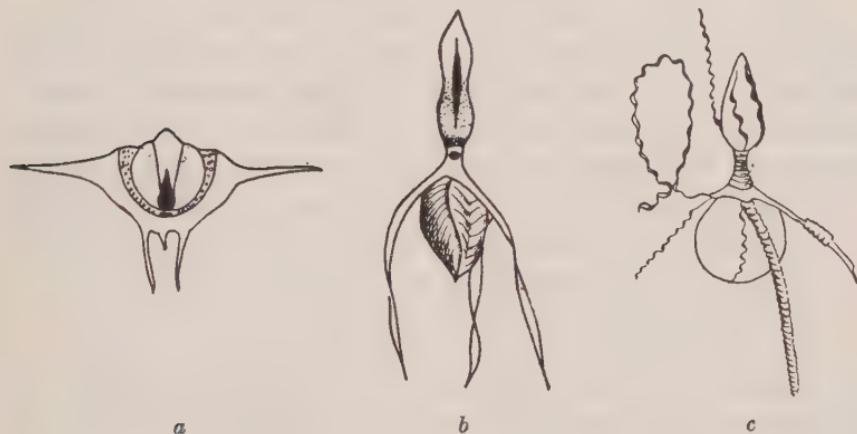


Fig. 146. Sperm-cells of Decapod crustacea (after Koltzoff). *a*, *Inachus scorpio*; *b*, *Galathea squamifera*; *c*, do. after maceration, to shew spiral fibrillae.

corpuscles in each is found, after a given time, to obey a certain law (Smoluchowsky's Law), defining the number of contacts of floating bodies under ordinary physical conditions*.

The sperm-cells of the Decapod crustacea exhibit various singular shapes. In the crayfish they are flattened cells with stiff curved processes radiating outwards like St Catherine's wheel; in *Inachus* there are two such circles of stiff processes; in *Galathea* we have a still more complicated form, with long and slightly twisted processes.

* Smoluchowsky, *Ztschr. f. physik. Chemie*, xcix, p. 129, 1917; Eric Ponder, On Rouleaux-formation, *Q. Journ. Exp. Physiol.* xvi, pp. 173-194, 1926.

In all these cases, just as in the case of the blood-corpuscle, the structure alters, and finally loses, its characteristic form when the constitution of the surrounding medium is changed*.

Here again, as in the blood-corpuscle, we have to do with the important force of osmosis, manifested under conditions similar to those of Pfeffer's classical experiments on the plant-cell†. The surface of the cell acts as a semi-permeable membrane, permitting the passage of certain dissolved substances (or their ions), and including or excluding others: and thus rendering manifest and measurable the existence of a definite "osmotic pressure." Again, in the hen's egg a delicate yolk-membrane separates the yolk from the white. The morphologist looks on it but as the cell-wall of a vast yolk-laden germ-cell; the physiologist sees in it a semi-permeable membrane, the seat of many complex activities. The end and upshot of these last is that a steady difference of osmotic pressure, the equivalent of some two atmospheres, is maintained between yolk and white; and yet there is no current flowing through. Somewhere or other in the system there is a constant metabolic flux, a continuous liberation of energy, a continual doing of work, all leading to the maintenance of a steady dynamical state, which is not "equilibrium‡."

In the case of the sperm-cells of *Inachus*, certain quantitative experiments have been performed. The sperm-cell exhibits its characteristic conformation while lying in the serous fluid of the animal's body, in ordinary sea-water, or in a 5 per cent. solution of potassium nitrate, these three fluids being all "isotonic" with one another. As we alter the concentration of potassium nitrate, the cell assumes certain definite forms corresponding to definite concentrations of the salt; and, as a further and final proof that the phenomenon is entirely physical, it is found that other salts produce an identical effect when their concentration is proportionate to their molecular weight, and whatever identical effect is produced

* Cf. N. K. Koltzoff, Studien über die Gestalt der Zelle, *Arch. f. mikrosk. Anat.* LXVII, pp. 365-572, 1905; *Biol. Centralbl.* XXIII, pp. 680-696, 1903; XXVI, pp. 854-863, 1906; XLVIII, pp. 345-369, 1928; *Arch. f. Zellforschung*, II, pp. 1-65, 1908; VII, pp. 344-423, 1911; *Anat. Anzeiger*, XLI, pp. 183-206, 1912.

† W. Pfeffer, *Osmotische Untersuchungen*, Leipzig, 1877.

‡ Cf. J. Straub, Der Unterschied in osmotischer Konzentration zwischen Eigelb und Eiklar, *Rec. Trav. Chim. du Pays-Bas*, XLVIII, p. 49, 1929.

by various salts in their respective concentrations, a similarly identical effect is produced when these concentrations are doubled or otherwise proportionately changed.

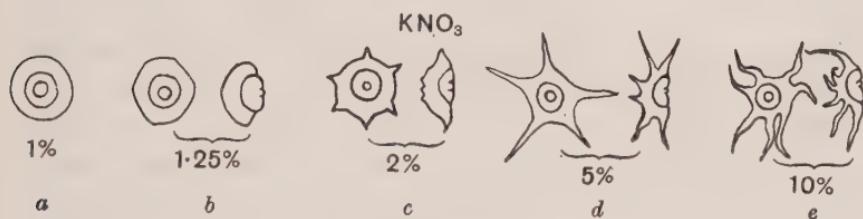


Fig. 147. Sperm-cells of *Inachus*, as they appear in saline solutions of varying density. After Koltzoff.

Thus the following table shews the percentage concentrations of certain salts necessary to bring the cell into the forms *a* and *c* of Fig. 147; in each case the quantities are proportional to the molecular weights, and in each case twice the quantity is necessary to produce the effect of *c*, compared with that which gives rise to the all but spherical form of *a*.

	% concentration of salts in which the sperm-cell of <i>Inachus</i> assumes the form of	
	<i>a</i>	<i>c</i>
Sodium chloride	0.6	1.2
Sodium nitrate	0.85	1.7
Potassium nitrate	1.0	2.0
Acetic acid	2.2	4.5
Cane sugar	5.0	10.0

If we look then upon the spherical form of this cell as its true condition of symmetry and of equilibrium, we see that what we call its normal appearance is just one of many intermediate phases of shrinkage, brought about by the abstraction of fluid from its interior as the result of an osmotic pressure greater outside than inside the cell, and where the shrinkage of *volume* is not kept pace with by a contraction of the *surface-area*. In the case of the blood-corpusele, the shrinkage is of no great amount, and the resulting deformation is symmetrical; such structural inequality as may be necessary to account for it need be but small. But in the case of the sperm-cells, we must have, and we actually do find, a somewhat

complicated arrangement of more or less rigid or elastic structures in the wall of the cell, which, like the wire framework in Plateau's experiments, restrain and modify the forces acting on the drop. In one form of Plateau's experiments, instead of supporting his

drop on rings or frames of wire, he laid upon its surface one or more elastic coils; and then, on withdrawing oil from the centre of his globule, he saw its uniform shrinkage counteracted by the spiral springs, with the result that the centre of each elastic coil seemed to shoot out into a prominence. Just such spiral coils are figured (after Koltzoff) in Fig. 148*; and they may be regarded as closely akin to those

Fig. 148. Sperm-cell of *Dromia*. After Koltzoff.

local thickenings or striations, spiral and other, which are common in vegetable cells.

Physically speaking, the protoplasmic colloids are neither simple nor uniform. We begin by thinking of our cell as a *drop* of a homogeneous fluid and on this bold simplifying assumption we account for its form to a first, and often to a near, approximation. For the cell is largely composed of fluid "hydrosols," which are still fluid however viscous they may be, and still tend towards rounded, drop-like configurations. But it has also its "hydrogels," which shew a certain tenacity, a certain elasticity, a certain reluctance to let their particles move on one another; and of these are formed the scarce distinguishable fibrillae within a host of highly specialised cells, the elastic fibres of a tendon, the incipient cell-walls of a plant, the rudiments of many axial and skeletal structures.

The cases which we have just dealt with lead us to another consideration. In a semi-permeable membrane, through which water passes freely in and out, the conditions of a liquid surface are greatly modified; in the ideal or ultimate case, there is neither surface nor surface-tension at all. And this would lead us some-

* As Bethe points out (*Zellgestalt, Plateausche Flüssigkeitsfigur und Neuro-fibrille, Anat. Anz.* XL, p. 209, 1911), the spiral fibres of which Koltzoff speaks must lie *in the surface*, and not within the substance, of the cell whose conformation is affected by them.



what to reconsider our position, and to enquire whether the true surface-tension of a liquid film is actually responsible for *all* that we have ascribed to it, or whether certain of the phenomena which we have assigned to that cause may not in part be due to the contractility of definite and elastic membranes. But to investigate this question, in particular cases, is rather for the physiologist: and the morphologist may go his way, paying little heed to what is no great difficulty. For in surface-tension we have the production of a film with the properties of an elastic membrane, and with the special peculiarity that contraction continues with the same energy however far the process may have already gone; while the ordinary elastic membrane contracts to a certain extent, and contracts no more. But within wide limits the essential phenomena are the same in both cases. Our fundamental equations apply to both cases alike. And accordingly, so long as our purpose is *morphological*, so long as what we seek to explain is regularity and definiteness of form, it matters little if we should happen, here or there, to confuse surface-tension with elasticity, the contractile forces manifested at a liquid surface with those which come into play at the complex internal surfaces of an elastic solid.

CHAPTER VI

A NOTE ON ADSORPTION

AN important corollary to, or amplification of, the theory of surface-tension is to be found in the chemico-physical doctrine of Adsorption; which means, in a word, the concentration of a substance *at a surface*, by reason of that *surface-energy* of which we have had so much to say*. Charcoal, with its vast internal surface-area of carbonised cell-walls, is the commonest and most familiar of adsorbents, and of it Du Bois Reymond first used the name. In its full statement this subject becomes very complicated, and involves physical conceptions and mathematical treatment which go far beyond our range. But it is necessary for us to take account of the phenomenon, even though it be in the most elementary way.

In the brief account of the theory of surface-tension with which our last chapter began, it was shewn that, in a drop of liquid, the potential energy of the system could be diminished, and work manifested accordingly, in two ways. In the first place we saw that, at our liquid surface, surface-tension tends to set up an equilibrium of form, in which the surface is reduced or contracted either to the absolute minimum of a sphere, or at any rate to the least possible area which is permitted by the various circumstances and conditions; and if the two bodies which comprise our system, namely the drop of liquid and its surrounding medium, be simple substances, and the system be uncomplicated by other distributions of force, then the energy of the system will have done its work when this equilibrium of form, this minimal area of surface, is once attained. This phenomenon of the production of a minimal surface-area we have now seen to be of fundamental importance in the external

* Some define adsorption as surface-condensation, without reference to the forces which produce it; in other words they recognize chemical, electrical and other forces, including cohesion, as producing analogous or indistinguishable results: cf. A. P. Mathews, in *Physiological Reviews*, 1, pp. 553–597, 1921.

morphology of the cell, and especially (so far as we have yet gone) of the solitary cell or unicellular organism.

But we also saw, according to Gauss's equation, that the potential energy of the system will be diminished (and its diminution will accordingly be manifested in work) if from any cause the specific surface-energy be diminished, that is to say if it be brought more nearly to an equality with the specific energy of the molecules in the interior of the liquid mass. This latter is a phenomenon of great moment in physiology, and, while we need not attempt to deal with it in detail, it has a bearing on cell-form and cell-structure which we cannot afford to overlook.

A diminution of the surface-energy may be brought about in various ways. For instance, it is known that every isolated drop of fluid has, under normal circumstances, a surface-charge of electricity: in such a way that a positive or negative charge (as the case may be) is inherent in the surface of the drop, while a corresponding charge, of contrary sign, is inherent in the immediately adjacent molecular layer of the surrounding medium. Now the effect of this distribution, by which all the surface molecules of our drop are similarly charged, is that by virtue of the charge they tend to repel one another, and possibly also to draw other molecules, of opposite charge, from the interior of the mass; the result being in either case to antagonise or cancel, more or less, that normal tendency of the surface molecules to attract one another which is manifested in surface-tension. In other words, an increased electrical charge concentrating at the surface of a drop tends, whether it be positive or negative, to *lower* the surface-tension.

Again, a rise of temperature diminishes surface-tension, and consequently facilitates the formation of a bubble or a froth. It follows (from the principle of Le Chatelier) that foam is warmer than the fluid of which it is made, and the difference is all the greater the lower the concentration of the foaming (or capillary-active) substance*.

But a still more important case has next to be considered. Let us suppose that our drop consists no longer of a single chemical substance, but contains other substances either in suspension or in solution. Suppose (as a very simple case) that it be a watery

* Cf. Fr. Schütz, in *Nature*, April 10, 1937. In the case of 0·01 per cent. solution of saponin, the temperature-difference is no less than 3·3° C.

fluid, exposed to air, and containing droplets of oil: we know that the specific surface-tension of oil in contact with air is much less than that of water, and it follows that, if the watery surface of our drop be replaced by an oily surface the specific surface-energy of the system will be notably diminished. Now under these circumstances it is found that (quite apart from gravity, which might cause it to *float* to the surface) the oil has a tendency to be *drawn* to the surface; and again this phenomenon of molecular attraction or adsorption represents work done, equivalent to the diminished potential energy of the system*. In more general terms, if a liquid be a chemical mixture, some one constituent in which, if it entered into or increased in amount in the surface layer, would have the effect of diminishing its surface-tension, then that constituent will have a tendency to accumulate or concentrate at the surface: the surface-tension may be said, as it were, to exercise an attraction on this constituent substance, drawing it into the surface-layer, and this tendency will proceed until at a certain "surface-concentration" equilibrium is reached, its opponent being that osmotic force which tends to keep the substance in uniform solution or diffusion. In other words, in any "two-phase" system, a change of concentration at the boundary-surface and a diminution of surface-tension there accompany one another of necessity; positive adsorption means negative surface-tension, and *vice versa*. Furthermore, the lowering of surface-tension (as by saponin) will permit (*caeteris paribus*) an extension of surface, manifesting itself in "froth." Thus the production of a froth and the concentration of appropriate substances therein are two sides of one and the same phenomenon.

In the complex mixtures which constitute the protoplasm of the living cell, this phenomenon of adsorption has abundant play: for many of its constituents, such as fats, soaps, proteins, lecithin, etc., possess the required property of diminishing surface-tension.

* The first instance of what we now call an adsorptive phenomenon was observed in soap-bubbles. Leidenfrost was aware that the outer layer of the bubble was covered by an "oily" layer (*De aquae communis nonnullis qualitatibus tractatus*, Duisburg, 1756). A hundred years later Dupré shewed that in a soap-solution the soap tends to concentrate at the surface, so that the surface-tension of a very weak solution is very little different from that of a strong one (*Théorie mécanique de la chaleur*, 1869, p. 376; cf. Plateau, II, p. 100).

Moreover, the more a substance has the power of lowering the surface-tension of the liquid in which it happens to be dissolved, the more will it tend to displace another and less effective substance from the surface-layer. Thus we know that protoplasm always contains fats, not only in visible drops, but also in the finest suspension or "colloidal solution"; and if under any impulse, such for instance as might arise from the Brownian movement, a droplet of oil be brought close to the surface, it is at once drawn into that surface and tends to spread itself in a thin layer over the whole surface of the cell. But a soapy surface (for instance) in contact with the surrounding water would have a surface-tension even less than that of the film of oil: and consequently, if soap be present in the water it will in turn be adsorbed, and will tend to displace the oil from the surface pellicle*. And all this is as much as to say that the molecules of the dissolved or suspended substance or substances will so distribute themselves throughout the drop as to lead towards an equilibrium, for each small unit of volume, between the superficial and internal energy; or, in other words, so as to reduce towards a minimum the potential energy of the system. This tendency to concentration at a surface of any substance within the cell by which the surface-tension tends to be diminished, or *vice versa*, constitutes, then, the phenomenon of *adsorption*; and the general statement by which it is defined is known as the Willard-Gibbs, or Gibbs-Thomson law†, and was arrived at not by experimental but by theoretical and hydrodynamical methods.

An assemblage of drops or droplets offers a great extension of surface, but so also does an assemblage of equally minute cells or

* This identical phenomenon was the basis of Quincke's theory of amoeboid movement (*Ueber periodische Ausbreitung von Flüssigkeitsoberflächen, etc.*, *SB. Berlin. Akad.* 1888, pp. 791–806; cf. *Pflüger's Archiv*, 1879, p. 136). We must bear in mind that to describe an amoeboid cell as "naked" does not imply that its outer layer is identical with its internal substance.

† J. Willard Gibbs, Equilibrium of heterogeneous substances, *Tr. Conn. Acad.* III, pp. 380–400, 1876, also in *Collected Papers*, I, pp. 185–218, London, 1906; J. J. Thomson, *Applications of Dynamics to Physics and Chemistry*, 1888 (Surface tension of solutions), p. 190. See also (*int. al.*) various papers by C. M. Lewis, *Phil. Mag.* (6), xv, p. 499, 1908; xvii, p. 466, 1909; *Zeitschr. f. physik. Chemie*, lxx, p. 129, 1910; Milner, *Phil. Mag.* (6), xiii, p. 96, 1907; A. B. Macallum, The role of surface-tension in determining the distribution of salts in living matter, *Trans. 15th Int. Congress on Hygiene, etc.*, Washington, 1912; etc.

pores; both alike are "two-phase" systems, and in both alike the phenomenon of adsorption has free play. The occlusion of gases, including water-vapour, by charcoal is a familiar phenomenon of adsorption, and is due to the minuteness of the pores only in so far as surface-area is increased and multiplied thereby. For surface-energy is surface-strain or surface-tension \times surface-area, and is vastly increased by minute subdivision. And surface-energy is such that, whenever a substance is introduced into a two-phase system—which merely means two things in touch (or surface-contact) with one another—it is apt to concentrate itself *on the surface* where the two phases meet. *Absorption* implies uniform distribution, as when a gas is absorbed by a liquid; *adsorption* implies a heterogeneous field, and a concentration localised on the surfaces therein.

Among the many important physical features or concomitants of this phenomenon, let us take note at present that we need not conceive of a strictly superficial distribution of the adsorbed substance, that is to say of its direct association with the surface-layer of molecules such as we imagined in the case of an electrical charge; but rather of a progressive tendency to concentrate more and more, the nearer the surface is approached. Indeed we may conceive the colloid or gelatinous precipitate in which, in the case of our protoplasmic cell, the dissolved substance tends often to be thrown down, to constitute one boundary layer after another, the general effect being intensified and multiplied by the repetition of these new surfaces.

Moreover, it is not less important to observe that the process of adsorption, in the neighbourhood of the surface of a heterogeneous liquid mass, is a process which *takes time*; the tendency to surface concentration is a gradual and progressive one, and will fluctuate with every minute change in the composition of our substance and with every change in the area of its surface. In other words, it involves (in every heterogeneous substance) a continual instability: and a constant manifestation of motion, sometimes in the mere invisible transfer of molecules, but often in the production of visible currents, or manifest alterations in the form or outline of the system.

Cellular activity is of necessity associated with cellular structure,

even in our simplest interpretation thereof, as a mere increase of surface due to the existence and the multiplication of cells. In the chemistry of the tissues there may be substances (catalysts and others) which exhibit their proper reactions even though the cells containing them be disintegrated or destroyed; but other processes, oxidation itself among them, are essentially surface-actions, based on adsorption at the vast cell-surface of the tissue*. The breaking-down of the cell-walls, the disintegration of cellular structure in a tissue, brings about "a biochemical chaos, a medley of reactions†." Cells are not merely there because the tissue has grown by their multiplication; there are physico-chemical reasons, even of an elementary kind, which render the morphological phenomenon of the cell indispensable to physiological action.

The physiologist deals with the surface-phenomena of the cell in ways undreamed of when I began to write this book. To begin with, the concept of a *surface* (in the old mathematical or quasi-mathematical sense) no longer suffices to describe the boundary conditions of even a "naked" protoplasmic cell. As Rayleigh foretold, and as Irving Langmuir has proved, the "boundary-state" consists of a layer of complex molecules, each one a long array of atoms, all set side by side in an orderly and uniform way. There is not merely a boundary-surface between two phases (as the older colloid chemistry supposed) but a *boundary-layer*, which itself constitutes a third phase, or interphase, and which part of the surface-energy has gone to the making of.

Surface-energy plays a leading part in modern theories of muscular contraction, and has indeed done so ever since FitzGerald and d'Arsonval indicated a connection between them some sixty years or more ago‡. It plays its part handsomely (we may be sure) in the electric pile of the Torpedo, where two million tiny discs present a

* Many surface-active substances are known to be among the most active pharmacologically; cf. Michaelis and Rona, *Physikal. Chemie*, 1930.

† A. V. Hill, *Proc. R.S.* (B), ciii, p. 138; cf. also M. Penrose and J. H. Quastel, on Cell structure and cell activity, *ibid.* cvii, p. 168.

‡ Cf. G. F. FitzGerald, On the theory of muscular contraction, *Brit. Ass. Rep.* 1878; also in *Scientific Writings*, ed. Larmor, 1902, pp. 34, 75. A. d'Arsonval, Relations entre l'électricité animale et la tension superficielle, *C.R.* cvi, p. 1740, 1888; A. Imbert, Le mécanisme de la contraction musculaire, déduit de la considération des forces de tension superficielle, *Arch. de Phys.* (5), ix, pp. 289–301, 1897; A. J. Ewart, *Protoplasmic Streaming in Plants*, Oxford, 1903, pp. 112–119.

vast aggregate of interfacial contact. It gives us a new conception, as Wolfgang Ostwald was the first to shew, of the relation of oxygen to the red corpuscles of the blood*. But many more and still more complicated "film-reactions" are started or intensified by the oriented molecules of the monolayer. The catalytic action of living ferments (a subject vast indeed) is largely a question of modified adsorption, or of surface-action. The range of bodies so adsorbed is extremely limited; the specific reactions, which depend on the bacterium engaged, are fewer still; and sometimes a whole class of substances may be adsorbed, and only one of them thrown specifically into action†. The physiological, and sometimes lethal, actions of various substances are examples of similar effects. The chemistry of the surface-layer in this cell or that may be elucidated by its reactions to various "penetrants," and depends somehow on the molecular orientation of the surfaces, and on the potentials associated with the characteristic electric fields which we may suppose to correspond to the particular molecular arrangements‡.

It is the dynamic aspect of the case, the ingresses, egresses and metabolic changes associated with the boundary-layer, which interest the physiologist. He finds the monolayer acting in ways not known in a homogeneous liquid—and adsorption is one of these ways. We keep as much as may be to the morphological side of the case rather than to the physiological, to the static side rather than to the dynamic, to the equilibrium attained rather than to the energies to which it is due. We continue to speak of surface, and of surface-

* Ueber die Natur der Bindung der Gase im Blut und in seinen Bestandteilen, *Kolloid Ztschr.* II, pp. 264–272, 1908; cf. Loewy, Dissociationsspannung des Oxyhaemoglobin im Blut, *Arch. f. Anat. u. Physiol.* 1904, p. 231. Arrhenius remarked long ago that the forces which produce adsorption are of the same order, and of the same nature, as those which cause the mutual attractions of the molecules of a gas. Hence the *order* is constant in which various gases are adsorbed by different adsorbents. The question of the inner mechanism of the forces which result in surface-tension, adsorption and allied phenomena, and their relation to electric charge on particles or ions, belongs to the highest parts of physical chemistry. Besides countless recent papers, M. v. Smoluchowski's Versuch einer mathematischen Theorie der Koagulationskritik, *Z. f. physik. Chemie*, XCII, pp. 129–168, 1918, is still interesting.

† Cf. N. K. Adams, *Physics and Chemistry of Surfaces*. 1930. Also (*int. al.*) J. H. Quastel, Mechanism of bacterial action, *Trans. Faraday Soc.* XXVI, pp. 831–861, 1930.

‡ This is Loeb's so-called "membrane-effect," cf. *Journ. Biol. Chemistry*, XXXII, p. 147, 1917; and J. Gray, *Journ. Physiol.* LIV, pp. 68–78, 1920.

energy and of adsorptive phenomena, in a somewhat old-fashioned way; but even with this simplifying limitation we find them helpful, throwing light upon our subject.

In the first place our preliminary account, such as it is, is already tantamount to a description of the process of development of a cell-membrane, or cell-wall. The so-called "secretion" of this cell-wall is nothing more than a sort of exudation, or striving towards the surface, of certain constituent molecules or particles within the cell; and the Gibbs-Thomson law formulates, in part at least, the conditions under which they do so. The adsorbed material may range from an almost unrecognisable pellicle to the distinctly differentiated "ectosarc" of a protozoon, and again to the development of a fully-formed cell-wall, as in the cellulose partitions of a vegetable tissue. In such cases, the dissolved and adsorptive material has not only the property of lowering the surface-tension, and hence of itself accumulating at the surface, but has also the property of increasing the viscosity and mechanical rigidity of the material in which it is dissolved or suspended, and so of constituting a visible and tangible "membrane*." The "zoogloea" around a group of bacteria is probably a phenomenon of the same order. In the superficial deposition of inorganic materials we see the same process abundantly exemplified. Not only do we have the simple case of the building of a shell or "test" upon the outward surface of a living cell, as for instance in a Foraminifer, but in a subsequent chapter, when we come to deal with spicules and spicular skeletons such as those of the sponges and of the Radiolaria, we shall see how highly characteristic it is of the whole process of

* We may trace the first steps in the study of this phenomenon to Melsens, who found that thin films of white of egg become firm and insoluble (*Sur les modifications apportées à l'albumine... par l'action purement mécanique, C.R.* xxxiii, p. 247; *Ann. de chimie et de physique* (3), xxxiii, p. 170, 1851); and Harting made similar observations about the same time. Ramsden investigated the same subject, and also the more general phenomenon of the formation of albuminoid and fatty membranes by adsorption, and found (*int. al.*) that on shaking white of egg practically all the albumin passes gradually into the froth; cf. his *Koagulierung der Eiweisskörper auf mechanischer Wege, Arch. f. Anat. u. Phys. (Phys. Abth.)*, 1894, p. 517; *Abscheidung fester Körper in Oberflächenschichten, Z. f. phys. Chem.* xlvi, p. 341, 1902; *Proc. R.S.* lxxii, p. 156, 1904. For a general review of the whole subject see H. Zanger, *Ueber Membranen und Membranfunktionen*, in Asher-Spiro's *Ergebnisse der Physiologie*, vii, pp. 99-160, 1908.

spicule-formation for the deposits to be laid down just in the "interfacial" boundaries between cells or vacuoles, and how the form of the spicular structures tends in many cases to be regulated and determined by the arrangement of these boundaries. The so-called *collenchyma*, in which an excess of cellulose is laid down around the angles of contact of adjacent cells, in a kind of exaggerated "bourrelet," is another case in point*.

No pure liquid ever forms a froth or foam. White of egg is no exception to the rule; for the albumin is somehow changed, or "denatured," and becomes a quasi-solid when we beat it up. But in the frothing liquid there must always be some admixture present to concentrate on, or be adsorbed by, the surfaces and interfaces of the other; and this dispersion must go on completely and uniformly, so as to leave the whole system homogeneous. The resulting diminution of surface-tension facilitates the subdivision of the bubbles and dispersion of the air; and the adsorbed surface-layer gives firmness and stability to the system. The sudden increase of surface diminishes, for the moment, the concentration, or "thickness" of the surface-layer; the tension rises accordingly, and the cycle of operations begins anew†.

In physical chemistry, a distinction is usually drawn between adsorption and *pseudo-adsorption*, the former being a *reversible*, the latter an irreversible or permanent phenomenon. That is to say, adsorption, strictly speaking, implies the surface-concentration of a dissolved substance, under circumstances which, if they be altered or reversed, will cause the concentration to diminish or disappear. But pseudo-adsorption includes cases, doubtless originating in adsorption proper, where subsequent changes leave the concentrated substance incapable of re-entering the liquid system. It is obvious that many (though not all) of our biological illustrations, for instance the formation of spicules or of permanent cell-membranes, belong to the class of so-called pseudo-adsorption phenomena. But the apparent contrast between the two is in the main a secondary one, and however important to the chemist is of little consequence to us.

While this brief sketch of the theory of membrane-formation is cursory and inadequate, it is enough to shew that the physical theory of adsorption tends in part to overturn, in part to simplify

* Cf. G. Haberlandt, Zelle u. Elementarorgane, *Biol. Centralbl.* 1925, p. 263.

† Cf. F. G. Donnan, Some aspects of the physical chemistry of interfaces, *Brit. Ass. Address* (Section B), 1923; *Nature*, Dec. 15, 22, 1923.

enormously, the older histological descriptions. We can no longer be content with such statements as that of Strasbürger, that membrane-formation in general is associated with the "activity of the kinoplasm," or that of Harper that a certain spore-membrane arises directly from the astral rays*. In short, we have easily reached the general conclusion that the formation of a cell-wall or cell-membrane is a chemico-physical phenomenon, which the purely objective methods of the biological microscopist do not suffice to interpret.

Having reached this conclusion we may wait patiently, and confidently, for more. But when the physico-chemical nature of these phenomena is admitted, and their dependence on adsorption recognised, or at least assumed, we have still to remember that the chemist himself is none too certain of his ground. He still finds it hard, now and then, to tell how far adsorption and direct chemical action go their way together, what parts they severally play, what shares they take in their intimate cooperation†.

If the process of adsorption, on which the formation of a membrane depends, be itself dependent on the power of the adsorbed substance to lower the surface-tension, it is obvious that adsorption can only take place when the surface-tension already present is greater than zero. It is for this reason that films or threads of creeping protoplasm shew little tendency, or none, to cover themselves with an encysting membrane; and that it is only when, in an altered phase, the protoplasm has developed a positive surface-tension, and has accordingly gathered itself up into a more or less spherical body, that the tendency to form a membrane is manifested, and the organism develops its "cyst" or cell-wall. The holes in a Globigerina-shell are there "to let the pseudopodia through." They may also be described as due to unequal distribution of surface-energy, such as to prevent shell-substance from being adsorbed here and there, and at the same time inducing a pseudopodium to emerge.

* Strasbürger, Ueber Cytoplasmastrukturen, etc., *Jahrb. f. wiss. Bot.* xxx, 1897; R. A. Harper, Kerntheilung und freie Zellbildung im Ascus, *ibid.*; cf. Wilson, *The Cell in Development*, etc., pp. 53-55.

† The "adsorption theory" of dyeing is a case in point, where the precise mode, or modes, of action seem still far from settled.

It is found that a rise of temperature greatly reduces the adsorbability of a substance, and this doubtless comes, either in part or whole, from the fact that a rise of temperature is itself a cause of the lowering of surface-tension. We may in all probability ascribe to this fact and to its converse, or at least associate with it, such phenomena as the encystment of unicellular organisms at the approach of winter, or the frequent formation of strong shells or membranous capsules in "winter-eggs."

Again, since a film or a froth (which is a system of films) can only be maintained by virtue of a certain viscosity or rigidity of the liquid, it may be quickly caused to disappear by the presence in its neighbourhood of some substance capable of materially reducing the surface-tension; for this substance, being adsorbed, may displace from the surface-layer a material to which was due the rigidity of the film. In this way a "bathytonic" substance, such as ether, causes most foams to subside, and the pouring oil on troubled waters not only calms the waves but still more quickly dissipates the foam of the breakers. In a very different order of things, the breaking up of an alveolar network, as at a certain stage in the nuclear division of the cell, may be due in part to just such a cause, as well as to the direct lowering of surface-tension by electrical agency.

Our last illustration has led us back to the subject of a previous chapter, namely to the visible configuration of the interior of the cell, in so far (at least) as it represents a "dispersed system," coarse enough to be visible; and in connection with this wide subject there are many phenomena on which light is apparently thrown by our knowledge of adsorption, of which we took little or no account in our former discussion. One of these phenomena is nothing less than that visible or concrete "polarity," which we have seen to be in some way associated with a dynamical polarity of the cell.

This morphological polarity may be of a very simple kind, as when it is manifested, in an epithelial cell, by the outward shape of the elongated or columnar cell itself, by the essential difference between its free surface and its attached base, or by the presence in the neighbourhood of the former of mucus or other products of the cell's activity: But in a great many cases, this polarised symmetry is supplemented by the presence of various fibrillae, or

of linear arrangements of particles, which in the elongated or "monopolar" cell run parallel with its axis, but tend to a radial arrangement in the more or less rounded or spherical cell. Of late years great importance has been attached to these various linear or fibrillar arrangements, as they are seen (*after staining*) in the cell-substance of intestinal epithelium, of spermatocytes, of ganglion cells, and most abundantly and frequently of all in gland cells. Various functions have been assigned, and hard names given to them; for these structures include your mitochondria* and your chondriokonts (both of these being varieties of chondriosomes), your Altmann's granules, your microsomes, pseudo-chromosomes, epi-

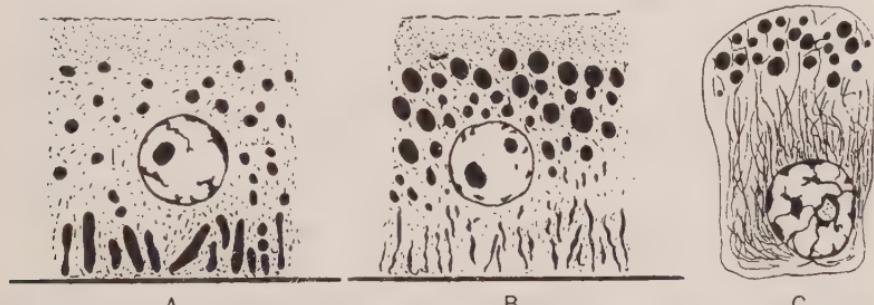


Fig. 149. A, B, Chondriosomes in kidney-cells, prior to and during secretory activity (after Barratt); C, do. in pancreas of frog (after Mathews).

dermal fibrils and basal filaments, your archeoplasm and ergastoplasm, and probably your idiozomes, plasmosomes, and many other histological minutiae†.

The position of these bodies with regard to the other cell-structures is carefully described. Sometimes they lie in the neighbourhood of the nucleus itself, that is to say in proximity to the fluid boundary surface which separates the nucleus from the

* Mitochondria are threads which move slowly through the protoplasm, sometimes break in two, and often tend to radiate from the centrosphere or division-centre of the cell. The nucleoli are two or more opaque bodies within the nucleus, which keep shifting their position; within the cytoplasm many small fatty bodies likewise move about, and display the Brownian oscillation.

† Cf. A. Gurwitsch, *Morphologie und Biologie der Zelle*, 1904, pp. 169–185; Meves, *Die Chondriosomen als Träger erblicher Anlagen*, *Arch. f. mikrosk. Anat.* 1908, p. 72; J. O. W. Barratt, Changes in chondriosomes, etc., *Q.J.M.S.* LVIII, pp. 553–566, 1913, etc.; A. P. Mathews, Changes in structure of the pancreas cell, etc., *Journ. Morph.* xv (Suppl.), pp. 171–222, 1899.

cytoplasm; and in this position they often form a somewhat cloudy sphere which constitutes the *Nebenkern*. In the majority of cases, as in the epithelial cells, they form filamentous structures, and rows of granules, whose main direction is parallel to the axis of the cell; and which may, in some cases, and in some forms, be conspicuous at the one end, and in some cases at the other end of the cell. But I seldom find the histologists attempting to explain, or to correlate with other phenomena, the tendency of these bodies to lie parallel with the axis, and perpendicular to the extremities of the cell; it is merely noted as a peculiarity, or a specific character, of these particular structures. Extraordinarily complicated and diverse functions have been ascribed to them. Engelmann's "Fibrillenkonus," which was almost certainly another aspect of the same phenomenon, was held by him and by cytologists like Breda and Heidenhain to be an apparatus connected in some unexplained way with the mechanism of ciliary movement. Meves looked upon the chondriosomes as the actual carriers or transmitters of heredity. Altmann invented a new aphorism, *Omne granulum e granulo*, as a refinement of Virchow's (or Remak's) *omnis cellula e cellula**; and many other histologists, more or less in accord, accepted the chondriosomes as important entities, *sui generis*, intermediate in grade between the cell itself and its ultimate molecular components. The extreme cytologists of the Munich school, Popoff, Goldschmidt and others, following Richard Hertwig, declaring these structures to be identical with "chromidia" (under which name Hertwig ranked all extra-nuclear chromatin), would assign them complex functions in maintaining the balance between nuclear and cytoplasmic material; and the "chromidial hypothesis," as every reader of cytological literature knows, has become a very abstruse and complicated thing†. With the help of the "binuclearity hypothesis" of Schaudinn and his school, it has given us the chromidial net, the

* Virchow, *Arch. f. pathol. Anat.* VIII, p. 23, 1855; but used, implicitly, by Remak, in his paper *Ueber extracelluläre Entstehung thierischer Zellen und über die Vermehrung derselben durch Theilung*, *Müller's Archiv*, 1852, pp. 47-57. That cells come, and only come, from pre-existing cells seems to have been clearly understood by John Goodsir, in 1846; see his *Anatomical Memoirs*, II, pp. 90, 389.

† Cf. Clifford Dobell, Chromidia and the binuclearity hypotheses; a review and a criticism, *Q.J.M.S.* LIII, pp. 279-326, 1909; A. Prenant, Les Mitochondries et l'Ergastoplasme, *Journ. de l'Anat. et de la Physiol.* XLVI, pp. 217-285, 1910 (both with copious bibliography).

chromidial apparatus, the trophochromidia, idiochromidiæ, gametochromidia, the protogonoplasm, and many other novel and original conceptions. There is apt to be confusion between important and unimportant things; and the very names are apt to vary somewhat in significance from one writer to another.

The outstanding fact, as it seems to me, is that physiological science has been heavily burdened in this matter, with a jargon of names and a thick cloud of hypotheses; but from the physical point of view we see but little mystery in the whole phenomenon. For, on the one hand, it is likely enough that these various bodies, by vastly extending the intra-cellular surface-area, may serve to increase the physico-chemical activities of the cell; and, on the other hand, we ascribe their very existence, in all probability and in general terms, to the "clumping" together under surface-tension of various constituents of the heterogeneous cell-contents, and to the drawing out of the little clumps along the axis of the cell towards one extremity or the other, in relation to osmotic currents as these are set up in turn in direct relation to the phenomena of surface-energy and of adsorption*. And all this implies that the study of these minute structures, even if it taught us nothing else, at least surely and certainly reveals the presence of a definite field of force, and a dynamical polarity within the cell†.

* Traube in particular has maintained that in differences of surface-tension we have the origin of the active force productive of osmotic currents, and that herein we find an explanation, or an approach to an explanation, of many phenomena which were formerly deemed peculiarly "vital" in their character. "Die Differenz der Oberflächenspannungen oder der Oberflächendruck eine Kraft darstellt, welche als treibende Kraft der Osmose, an die Stelle des nicht mit dem Oberflächendruck identischen osmotischen Druckes zu setzen ist, etc." (*Oberflächendruck und seine Bedeutung im Organismus, Pflüger's Archiv*, cv, p. 559, 1904.) There is, moreover, good reason to believe that physiological "osmosis" is not a general phenomenon common to this or that colloid membrane or dialyser, but depends (*int. al.*) on a specific affinity between the particular membrane (or the particular material it is moistened with) and the substance dialysed. This statement, made by Kahlenberg in 1906 (*Journ. Phys. Chem.* x, p. 141; also *Nature*, LXXV, p. 430, 1907), has been confirmed (e.g.) by R. Brinkmann and A. von Szent-Gyorgyi in *Biochem. Ztschr.* cxxxix, pp. 261-273, 1923.

† C. E. Walker, in an interesting paper on Artefacts as a guide to the chemistry of the cell, *Proc. R.S.* (B), ciii, pp. 397-403, 1928, tells how he took mixtures of albumen, gelatine and lipins, with droplets of methyl myristate (with or without phosphorus) to act as nuclei; and found on treating with osmic acid that the lipins had separated out and arranged themselves very much as do Golgi bodies and other structural elements in ordinary histological preparations.

Our next and last illustration of the effects of adsorption, which we owe to the work of the late Professor A. B. Macallum* of Montreal, is of great importance; for it introduces us to phenomena in regard to which we seem to stand on firmer ground than in some of the foregoing cases, albeit the whole story has not been told. In our last chapter we were restricted mainly, though not entirely, to a consideration of figures of equilibrium, such as the sphere, the cylinder or the unduloid; and we began at once to find ourselves in difficulties when we were confronted by departures from symmetry, even in such a simple case as the ellipsoidal yeast-cell and the production of its bud. We found the cylindrical cell of *Spirogyra*, with its plane partitions or its spherical ends, a simple matter to understand; but when this uniform cylinder puts out a lateral outgrowth in the act of conjugation, we have a new and very different system of forces to account for and explain. The analogy of the soap-bubble, or of the simple liquid drop, was apt to lead us to suppose that surface-tension was, on the whole, uniform over the surface of the cell; and that its departures from symmetry of form were due to variations in external resistance. But if we have been inclined to make such an assumption we must now reconsider it, and be prepared to deal with important localised variations in the surface-tension of the cell. For, as a matter of fact, the simple case of a perfectly symmetrical drop, with uniform surface, at which adsorption takes place with similar uniformity, is probably rare in physics, and rarer still (if it exist at all) in the fluid or fluid-containing system which we call in biology a cell. We have more to do with cells whose general heterogeneity of substance leads to qualitative differences of surface, and hence to varying distributions of surface-tension. We must accordingly investigate the case of a cell which displays some definite and regular heterogeneity of its liquid surface, just as *Amoeba* displays a heterogeneity which is complex, irregular and continually fluctuating in amount and distribution. Such heterogeneity as we are speaking of must be essentially chemical, and the preliminary problem is to devise methods of "microchemical" analysis, which shall reveal *localised* accumulations of particular substances within

* See his *Methoden u. Ergebnisse der Mikrochemie in der biologischen Forschung*; Asher-Spiro's *Ergebnisse*, VII, 1908.

the narrow limits of a cell, in the hope that, their normal effect on surface-tension being ascertained, we may then correlate with their presence and distribution the actual indications of varying surface-tension which the form or movement of the cell displays. In theory the method is all that we could wish, but in practice we must be content with a very limited application of it; for the substances which have such action as we are looking for, and which are also actual or possible constituents of the cell, are very numerous, while the means are very seldom at hand to demonstrate their precise distribution and localisation. But in one or two cases we have such means, and the most notable is in connection with the element potassium. As Macallum has shewn, this element can be revealed in very minute quantities by means of a certain salt, a nitrite of cobalt and sodium*. This salt penetrates readily into the tissues and into the interior of the cell; it combines with potassium to form a sparingly soluble nitrite of cobalt, sodium and potassium; and this, on subsequent treatment with ammonium sulphide, is converted into a characteristic black precipitate of cobaltic sulphide†.

By this means Macallum demonstrated, years ago, the unexpected presence of potassium (i.e. of chlorides or other potassium salts) accumulated in particular parts of various cells, both solitary cells and tissue cells‡; and he arrived at the conclusion that the localised accumulations in question were simply evidences of concentration of the dissolved potassium salts, formed and localised in accordance with the Gibbs-Thomson Law. For potassium (as we now know) has a much higher ionic velocity than sodium; and accordingly the

* On the distribution of potassium in animal and vegetable cells, *Journ. Physiol.* xxxii, p. 95, 1905. (The only substance at all likely to be confused with potassium in this reaction is creatine.)

† The reader will recognise a fundamental difference, and contrast, between such experiments as those of Macallum's and the ordinary staining processes of the histologist. The latter are (as a general rule) merely empirical, while the former endeavour to reveal the true microchemistry of the cell. "On peut dire que la microchimie n'est encore qu'à la période d'essai, et que l'avenir de l'histologie et spécialement de la cytologie est tout entier dans la microchimie": A. Prenant, Méthodes et résultats de la microchimie, *Journ. de l'Anat. et de la Physiol.* xlvi, pp. 343-404, 1910. There is an interesting paper by Brunswick, on the Limitations of microchemical methods in biology, in *Die Naturwissenschaften*, Nov. 2, 1923.

‡ It is always conspicuously absent, as are chlorides and phosphates in general, from the nuclear substance.

K-ions reach and occupy the adsorbing surfaces of the cell-membranes out of all proportion to their abundance in the external media*. And we may take it also that our potassium salts, like inorganic substances in general, tend to raise the surface-tension, and will be found concentrated, therefore, at a portion of the surface where the tension is weak†.



Fig. 150. Adsorptive concentration of potassium salts in (1) a cell of *Pleurocarpus* about to conjugate; (2) conjugating cells of *Mesocarpus*; (3) sprouting spores of *Equisetum*. After Macallum.

In Professor Macallum's figure (Fig. 150, 1) of the little green alga *Pleurocarpus*, we see that one side of the cell is beginning to bulge out in a wide convexity. This bulge is, in the first place, a sign of weakened surface-tension on one side of the cell, which as a whole had hitherto been a symmetrical cylinder; in the second place, we see that the bulging area corresponds to the position of a great concentration of the potassium salt; while in the third place,

* Cf. A. B. Macallum, Address to Section I, *Brit. Ass.* 1910; *Oberflächen-spannung und Lebenserscheinungen*, in Asher-Spiro's *Ergebnisse der Physiologie*, xi, pp. 598-688, 1911; also his important paper on Ionic mobility as a factor in influencing the distribution of potassium in living matter, *Proc. R.S.* (B), civ. pp. 440-458, 1929; cf. E. F. Burton, *Trans. Faraday Soc.* xxvi, p. 677, 1930.

† In accordance with the "principle of Le Chatelier," which is in fact a corollary to the Gibbs-Thomson Law.

from the physiological point of view, we call the phenomenon the first stage in the process of conjugation. In the figure of *Mesocarpus* (a close ally of *Spirogyra*), we see the same phenomenon admirably exemplified in a later stage. From the adjacent cells distinct outgrowths are being emitted, where the surface-tension has been weakened: just as the glass-blower warms and softens a small part of his tube to blow out the softened area into a bubble or diverticulum; and in our *Mesocarpus* cells (besides a certain amount of potassium rendered visible over the boundary which separates the green protoplasm from the cell-sap), there is a very large accumulation precisely at the point where the tension of the originally cylindrical cell is weakening to produce the bulge. But in a still later stage, when the boundary between the two conjugating cells is lost and the cytoplasm of the two cells becomes fused together, then the signs of potassium concentration quickly disappear, the salt becoming generally diffused through the now symmetrical and spherical "zygospore."

In a spore of *Equisetum*, while it is still a single cell, no localised concentration of potassium is to be discerned; but as soon as the spore has divided by an internal partition into two cells, the potassium salt is found to be concentrated in the smaller one, and especially towards its outer wall which is marked by a pronounced convexity. As this convexity (which corresponds to one pole of the now asymmetrical, or quasi-ellipsoidal spore) grows out into the root-hair, the potassium salt accompanies its growth and is concentrated under its wall. The concentration is, accordingly, a concomitant of the diminished surface-tension which is manifested in the altered configuration of the system.

The Acinete protozoa obtain their food through suctorial tentacles extruded from the surface of the cell: their extrusion being doubtless due to a local diminution of surface-tension. A dense concentration of potassium reveals itself, accordingly, in the surface-film of each tiny tentacle. As the tentacles are withdrawn their potassium diffuses into the cytoplasm; when retraction is complete it is again found in surface-concentration, but the surface-films on which it now concentrates are the surfaces of the protein-spherules (or "food-vacuoles") within the body of the cell.

In the case of ciliate or flagellate cells, there is to be found a

characteristic accumulation of potassium at and near the base of the cilia. The relation of ciliary movement to surface-tension* lies beyond our range, but the fact which we have just mentioned throws light upon the frequent or general presence of a little protuberance of the cell-surface just where a flagellum is given off (cf. p. 406), and of a little projecting ridge or fillet at the base of an isolated row of cilia, such as we find in *Vorticella*.

Yet another of Professor Macallum's demonstrations, though its interest is mainly physiological, will help us somewhat further to comprehend what is implied in our phenomenon. In a normal cell of *Spirogyra*, a concentration of potassium is revealed along the whole surface of the spiral coil of chlorophyll-bearing, or "chromatophoral," protoplasm, the rest of the cell being wholly destitute of that substance: the inference being that at this particular boundary, between chromatophore and cell-sap, the surface-tension is small in comparison with any other interfacial surface within the system. And again, in certain minute *Chytridia*-like fungi, parasitic on *Spirogyra* and the like, the potassium-reaction helps to trace the delicate haustoria of the parasite in their course within the host-cell — a clear indication of low surface-tension at the surface between.

Now as Macallum points out, the presence of potassium is known to be a factor, in connection with the chlorophyll-bearing protoplasm, in the synthetic production of starch from CO_2 under the influence of sunlight; but we are left in some doubt as to the consecutive order of the phenomena. For the lowered surface-tension, indicated by the presence of the potassium, may be itself a cause of the carbohydrate synthesis; while on the other hand, this synthesis may be attended by the production of substances (e.g. formaldehyde) which lower the surface-tension, and so conduce to the concentration of potassium. All we know for certain is that the several phenomena are associated with one another, as apparently inseparable parts or inevitable concomitants of a certain complex action†.

* Cf. J. Gray, The mechanism of ciliary movement, *Proc. R.S. (B)*, 1922–24.

† The distribution of potassium within plant-cells is more complicated than it seemed at first to be; but it is still the general if not the invariable rule to find it associated (by adsorption) with one boundary-surface or another. Cf. E. S. Dowding, Regional and seasonal distribution of potassium in plant tissues, *Ann. Bot.* xxxix, pp. 459–476, 1925. The whole question, first adumbrated by Macallum,

And now to return, for a moment, to the question of cell-form. When we assert that the form of a cell (in the absence of mechanical pressure) is essentially dependent on surface-tension, and even when we make the preliminary assumption that protoplasm is essentially a fluid, we are resting our belief on a general consensus of evidence, rather than on compliance with any one crucial definition. The simple fact is that the agreement of cell-forms with the forms which physical experiment and mathematical theory assign to liquid surfaces under the influence of surface-tension is so frequently and often so typically manifested that we are led, or driven, to accept the surface-tension hypothesis as generally applicable and as equivalent to a universal law. The occasional difficulties or apparent exceptions are such as to call for further enquiry, but fall short of throwing doubt on the hypothesis. Macallum's researches introduce a new element of certainty, a "nail in a sure place," when they demonstrate that in certain movements or changes of form which we should naturally attribute to weakened surface-tension, a chemical concentration which would naturally accompany such weakening actually takes place. They further teach us that in the cell a chemical heterogeneity may exist of a very marked kind, certain substances being accumulated here and absent there, within the narrow bounds of the system.

Such localised accumulations can as yet only be demonstrated in the case of a very few substances, and of a single one in particular; and these few are substances whose presence does not produce, but whose concentration tends to follow, a weakening of surface-tension. The physical cause of the localised inequalities of surface-tension remains unknown. We may assume, if we please, that they are due to the prior accumulation, or local production, of bodies which have this direct effect; though we are by no means limited to this hypothesis. But in spite of some remaining difficulties and uncertainties, we have arrived at the conclusion, as regards unicellular organisms, that not only their general configuration but also *their*

is part of the general subject of *ionic regulation*, which has since become a matter of great physiological importance; cf. (*int. al.*) D. A. Webb, Ionic regulation in *Carcinus moenas*, *Proc. R.S.* (B), cxxix, pp. 107-136, 1940, and many works quoted therein. It is curious and interesting that Macallum's first work on unequal ionic distribution in the tissues and Donnan's fundamental conception of the Donnan equilibrium (*Journ. Chem. Soc.* xcix, p. 1554, 1911) came just at the same time.

departures from symmetry may be correlated with the molecular forces manifested in their fluid or semi-fluid surfaces.

Looking at the physiological side, rather than at the morphological which is more properly our own, we see how very important a *cellular system* is bound to be, even in respect of its surface-area alone. The order of magnitude of the cells which constitute our tissues is such as to give a relation of surface to volume far beyond anything in all the structures or mechanisms devised and fabricated by man. At this extensive surface, capillary energy, a form of energy scarcely utilised by man, plays a large predominant part in the energetics of the organism. Even the warm-blooded animal is not in reality a heat-engine; working as it does at almost constant temperatures its output of energy is bound, by the principle of Carnot, to be small. Nor is it an electrostatic machine, nor yet an electrodynamic one. It is a mechanism in which chemical energy turns into surface-energy, and, working hand in hand, the two are transformed into mechanical energy, by steps which are for the most part unknown*.

We are led on by these considerations to reflect on the molecular, rather than the histological, structure of the cell. We have already spoken in passing of "monomolecular layers," such as Henri Devaux imagined some thirty years ago, and afterwards obtained†, and such as Irving Langmuir has lately made his own. The free surface of every liquid (provided the form and symmetry of its molecules permit) presents a single layer of oriented molecules. Such a surface is no mere limit or simple boundary; it becomes a region of great importance and peculiar activity in certain cases, when, for instance, protein molecules of vast complexity are concerned. It is then a morphological field with a molecular structure of its own, and a dynamical field with energetics of its own. It becomes a frontier where this alien molecule may be excluded and that other be passed through: where some must submit to mere adsorption, and others suffer chemical change. In a word, we begin to look on a surface-layer or membrane, visible or invisible, as a vastly important thing, a place of delicate operations, and a field of peculiar and potent activity.

* Lippmann imagined a *moteur électrocapillaire*, unique in the history of mechanical invention. Cf. Berthelot, *Rev. Sci.* Dec. 7, 1913.

† Cf. (*int. al.*) H. Devaux, *La structure moléculaire de la cellule végétale*, *Bull. Soc. Bot. de France*, LXXV, p. 88, 1928.

